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COMITÉ DE RÉDACTION

P. H. CHRISTENSEN, K. GÖSSWALD, P.-P. GRASSÉ,
C. JUCCI, A. RAINIER, T. C. SCHNEIRLA, T. UCHIDA

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I

MÉMOIRES ORIGINAUX

MORPHOLOGIE ET COMPORTEMENT DES FOURMIS LESTOBIOTIQUES DU GENRE *EPIXENUS* EMERY

par

Francis BERNARD

En 1908, EMERY créait le genre *Epixenus* pour l'*E. andrei* Em., trouvé en Palestine dans un nid de *Monomorium venustum* Sm., et décrit sommairement par ANDRÉ (1881) comme une ♀ anormale de ce *Monomorium*. *Epixenus* est d'ailleurs très voisin des *Monomorium*, dont il diffère surtout par les pétioles des ♀, très dilatés en écaille. En 1910, FOREL décrivait *E. biroï*, sur des ♀ prises dans le nid de *Monomorium creticum* Em. (= *Salomonis* L.).

Cette particularité des pétioles caractérisant presque toujours des Myrmicins parasites ou lestobiotiques, EMERY rangeait les *Epixenus* dans cette catégorie et, dans son *Genera* (1922) écrivait (p. 185) « Ouvrière inconnue; elle n'existe vraisemblablement pas. »

En 1942, ma première année en Algérie, je découvris assez communément, aux environs d'Alger, une forme nouvelle qui va être décrite ci-dessous et dont les ouvrières étaient abondantes. Des observations plus récentes (mai 1955) permettent d'affirmer que cette espèce n'est pas toujours lestobiotique et possède le plus souvent des nids indépendants bien constitués. En outre, un autre *Epixenus* inédit (*E. guineensis* Bernard) avait été décrit en 1952 sur des ouvrières récoltées par M. LAMOTTE aux monts Nimba (Guinée).

Donc, *Epixenus* possède les trois castes, au moins chez 2 des 5 espèces actuellement admises, et est aussi bien éthiopien que méditerranéen du Sud. Il m'a semblé utile, au stade actuel de nos connaissances, de publier une courte monographie de ce genre, très peu connu encore, avec le résumé des observations sur *E. algiricus* n. sp., seule forme suivie sur le terrain, la seule aussi dont les larves aient été capturées :

1^o DIAGNOSE D'*EPIXENUS ALGIRICUS* N. SP. (fig. 1)

OUVRIÈRES :

Types. — 12 ♀ prises dans le même nid à Kaddous, à 7 kilomètres au sud d'Alger, sur une colline à Lentisques et argile en forte pente (altitude 150 mètres). Mars 1945.

Cotypes. — Plus de 200 ♀ prises, soit à Kaddous, soit dans la forêt de Baïnem, à 380 mètres d'altitude, à 6 kilomètres à l'ouest d'Alger, sol argileux horizontal. Les ♀ sont très uniformes et diffèrent très peu d'une station à l'autre. 1947 à 1955.

Taille : 2^{mm},2 à 2^{mm},5 (tandis que les races locales de *Monomorium salomonis* (L.) ont toutes de 2^{mm},5 à 2^{mm},8). L'allure et la démarche sont tout à fait celles de ce *Monomorium*.

Dessus du corps bien luisant, d'un brun foncé presque noir chez les individus âgés, d'un brun rougeâtre chez les immatures. Les fémurs et les scapes sont presque aussi foncés. De teinte plus claire sont les funicules, les tibias et les tarsi, tous d'un jaune foncé ou roux clair. Les mandibules sont jaune clair, avec leurs dents et un fin liséré au bord externe d'un brun noir. Dessous du corps brun clair.

Côtés de la tête en entier, son tiers postérieur dorsal et tout le thorax finement et élégamment réticulés. Entre les mailles de cette réticulation, très égales entre elles, le tégument est lisse et luisant. Les deux tiers antérieurs de la tête ont de fines stries longitudinales qui divergent en arrière vers les yeux et passent insensiblement à la réticulation très peu après le niveau des yeux. Il n'y a pas d'aire lisse au milieu de la tête, mais de l'aire frontale (petite cordiforme, lisse ou faiblement ponctuée) part vers l'arrière un court sillon lisse assez enfoncé, qui se termine par un point ovale enfoncé entre les milieux des yeux. Pétioles faiblement ponctués, gastre lisse et brillant, sauf à son bord antérieur, qui est un peu réticulé.

Pilosité très faible sur le corps : quelques grands poils raides, blanc jaunâtre, sur le clypéus, le pétiole et le gastre ; pas de pubescence. Pattes et appendices à courte pilosité blanchâtre, éparses.

Tête très convexe, longue de 0^{mm},75 (sans les mandibules) et large de 0^{mm},65 (chez *M. salomonis*, elle a en moyenne : longueur 0,80, largeur 0,75). Bords subparallèles, à peine élargis au niveau des yeux, qui sont un peu en avant du milieu de la tête. Vertex rectiligne, non rebordé. Yeux ovoïdes, très peu convexes, de 55 à 65 facettes. Scape court, dépassant à peine le bord postérieur de la tête.

Funicule moyen, son premier article égal aux trois suivants réunis. Les articles 2 à 7 aussi larges ou un peu plus larges que longs, l'article 8 et ceux de la massue nettement plus longs que larges.

Dessus du thorax peu convexe, assez rétréci au niveau du sillon méso-

épinotal, qui est large, superficiel et cannelé en long. Epinotum deux fois plus long que large, son bord postérieur rectiligne, ses angles postérieurs émoussés, sa face déclive un tiers plus courte que sa face antérieure.

Monomorium salomonis est très analogue, mais chez lui tous les articles du funicule sont bien plus longs que larges, la tête n'a pas de sillon longitudinal médian après l'aire frontale, le corps est bien moins luisant et, surtout, les pétioles sont plus étroits (fig. 1, e).

Le pétiole possède un pédoncule aplati, roux, translucide, aussi long que la moitié postérieure élargie. Celle-ci, aussi large que longue, est très convexe en dessous, mais à angle supérieur émoussé.

Post-pétiole environ d'un cinquième plus large que le pétiole; son nœud, de même profil que le premier nœud, est également noir et faiblement ponctué.

FEMELLES (reines désailées prises dans les nids) :

Types. — 7 reines de Kaddous, d'une seule fourmilière très peuplée. Mars 1945.

Cotypes. — 4 reines de la forêt de Baïnem, très semblables aux types. Une seule ♀ dans chacun des nids fouillés, sauf un nid contenant 2 reines, mais il y en avait peut-être d'autres en profondeur.

Taille : 3^{mm},8 à 4^{mm},1 (les reines de *M. salomonis* ont 5^{mm},2 à 5^{mm},8, elles sont donc relativement plus grandes que les ♂ par rapport à *Epixenus*). Le volume du gastre de la reine de *Monomorium* est plus que double de celui d'*Epixenus*.

Couleur très analogue à celles des ♂, mais pilosité plus forte, épinotum plus anguleux, pétioles encore plus dilatés et funicule légèrement plus allongé. La teinte générale est d'un noir plus foncé que celui des ♂ âgées, et la cuticule est plus lisse.

Tête subcarrée, bien moins sculptée que chez l'♂ : quelques stries longitudinales effacées vers le milieu du tiers antérieur, une vague réticulation aux angles postérieurs, le reste presque lisse.

Yeux très peu convexes, d'environ 110 facettes, placés très peu en avant du milieu de la tête. Ocelles arrondis, une légère dépression triangulaire entoure l'ocelle antérieur.

Comme chez l'♂, un court et large sillon médian part de l'aire frontale et sa longueur est sensiblement égale à celle d'un œil. Ce sillon a un peu la forme d'un point d'exclamation renversé. Vertex faiblement concave.

Le scape n'atteint pas, en arrière, le bord postérieur de la tête. Au funicule, les articles 2 à 7 sont un peu plus longs; aucun n'est plus large que long, mais presque tous sont subcarrés. Thorax plus luisant, plus convexe et bien plus élargi vers l'avant que celui de *Monomorium*. Surface ornée d'une réticulation à peine visible, effacée. Pronotum très convexe, arrondi, presque deux fois plus large que l'épinotum. Mésonotum ovale, plan en dessus,

2,5 fois plus long que large. Métanotum rougeâtre, aussi large que long, avec une forte gibbosité longitudinale tout le long de son tiers médian.

Segment médiaire aussi nettement réticulé que chez l'♀. L'épinotum, subtriangulaire en dessus, a sa moitié antérieure convexe et sa zone postérieure un peu concave. Angles postérieurs très marqués, arrondis, mais relevés et légèrement dentiformes. Pétioles proportionnellement un tiers plus larges que ceux de l'♀, leurs nœuds dilatés en écailles, mais le sommet de ces écailles est tronqué, émoussé, finement et peu densément ponctué. Elles sont loin d'être aussi tranchantes que les écailles des *Formicinæ*.

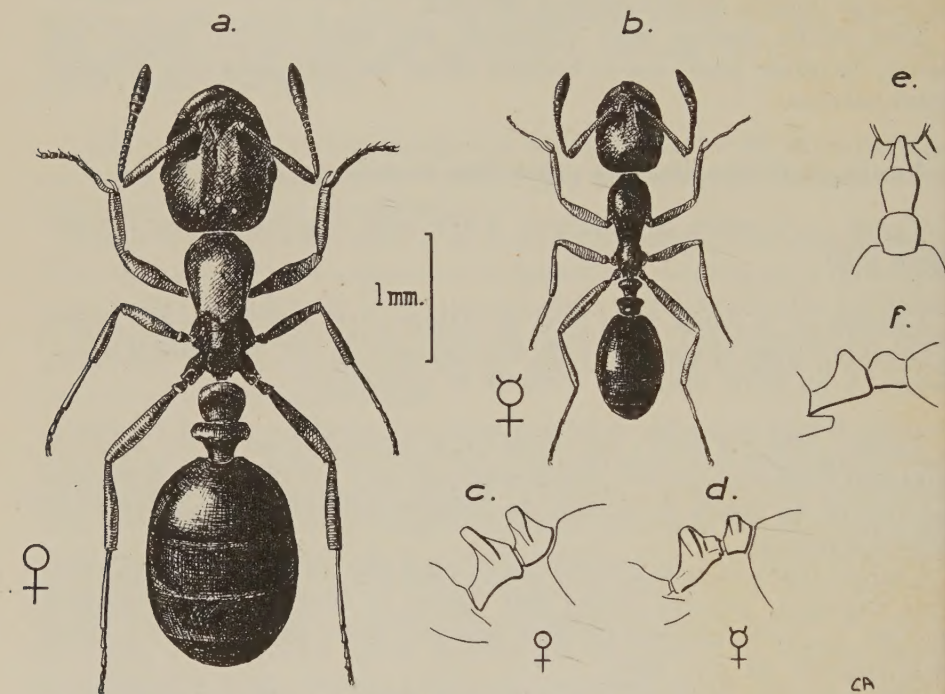


Fig. 1. — *Epixenus algericus* n. sp., des environs d'Alger. — a, reine, de la forêt de Bainem, longueur 4 millimètres; b, ouvrière, longueur 2^{mm},3; c, pétioles de la reine, vus de profil; d, pétioles de l'ouvrière; e, pétioles de face et, f, de profil, chez une ouvrière de *Monomorium salomonis* (L.) [voisine d'*Epixenus* et parfois pillée par lui].

C. AF

Pilosité bien plus développée que chez l'♂. Vers chaque angle postérieur de la tête, un grand poil tactile blanc, dressé, avec fossette piligère. Sur le métanotum et sur chacun des pétioles, 4 à 12 poils analogues, accompagnés de plus petits. Il y en a 16 à 20 en arrière de chaque tergite abdominal. Sur la tête, une pilosité banale courte, très espacée, blanchâtre. Poils couchés des appendices un peu plus serrés que ceux des ouvrières.

En résumé, les reines sont d'un tiers plus courtes que celles de *Monomorium* et d'aspect bien différent. Elles sont agiles, peu craintives, et il doit y en avoir plusieurs dans les fourmilières âgées, comme celle de Kaddous.

où j'avais pris huit femelles fécondes. Cette polygynie est également le cas chez la plupart des *Monomorium* nord-africains.

MALES :

Aucun mâle d'*Epixenus* n'est décrit avec certitude. *E. creticus* (EMERY, 1908) est basé sur un ♂ de Crète, et son appartenance à ce genre est douteuse. De mon côté, j'ai pris au fort des Arcades, au-dessus d'Alger, un ♂ pouvant se rattacher à *Epixenus*, mais il est très fortement ponctué et plus gros que les ♀, ce qui n'est le cas chez aucun *Monomorium*. On attendra donc des captures authentiques dans le nid pour identifier ce sexe.

2° MORPHOLOGIE LARVAIRE D'*EPIXENUS ALGIRICUS* (fig. 2)

Les larves de Fourmis sont encore mal connues, si on les compare aux larves de Sphérides, d'Abeilles, de Vespides, qui ont fait l'objet de nombreuses monographies. Bien des espèces et même des genres classiques de la région méditerranéenne n'ont pas encore leurs larves décrites.

Pourtant, malgré l'uniformité apparente de ces stades apodes, W. M. WHEELER (1918) avait raison d'insister sur leur intérêt biologique. Il a été le premier à montrer que la structure larvaire varie beaucoup avec les tribus et que des sous-familles évoluées comme les *Formicinae* ont encore des larves primitives.

De 1923 à aujourd'hui paraissent les publications très précises de G. C. WHEELER, apportant d'excellentes figures sur de nombreux genres américains. Dans mon propre laboratoire, H. GANTÉS (1949) a fait une bonne étude sur les larves de seize genres d'Algérie et leur croissance. C. ATHIAS-HENRIOT (1948) et S. VALENTINI (1951) ont contribué fructueusement à l'anatomie des larves.

De tous ces travaux (environ 14 références de valeur sur ce sujet), on peut déduire que l'étude des larves aidera beaucoup à comprendre l'évolution et l'écologie des Fourmis. Généralement, leur morphologie est assez différente d'une espèce à l'autre pour que l'on puisse établir (plus tard) des tableaux de détermination des larves, basés surtout, dans un même genre, sur la pilosité du corps et la structure des pièces buccales. L'anatomie et la croissance sont assez variables selon les espèces pour qu'elles jouent un rôle incontestable dans l'adaptation des Fourmis au milieu. C. ATHIAS-HENRIOT a prouvé que les trois *Messor* examinés par elle ont des conformations très diverses du tube digestif larvaire. H. GANTÉS a montré que certaines formes du désert (*Monomorium gracillimum*, *Cataglyphis albicans*) ont des larves néonates d'une grosseur exceptionnelle, adaptation probable à l'aridité locale par une moindre surface relative de leur corps.

Je dispose jusqu'à présent de deux séries de larves d'*Epixenus*, prises en mai 1955 dans les nids de la forêt de Bainem :

3 grosses larves de 1^{mm},7 à 1^{mm},9 ;
12 larves de 1^{mm},15 à 1^{mm},30.

Par comparaison avec *Monomorium salomonis*, qui a cinq stades larvaires comme la plupart des Fourmis, il est probable que les petites larves représentent le stade 2 et les grosses le stade 3. A part la taille, leurs morphologies sont très semblables (fig. 2) :

Tête bien différenciée, au moins autant que chez une larve de *Monomorium*, avec mandibules jaunes très visibles. Corps blanc au stade 2, jaunâtre ou brunâtre au stade 3. Les 3 segments thoraciques ont leurs limites

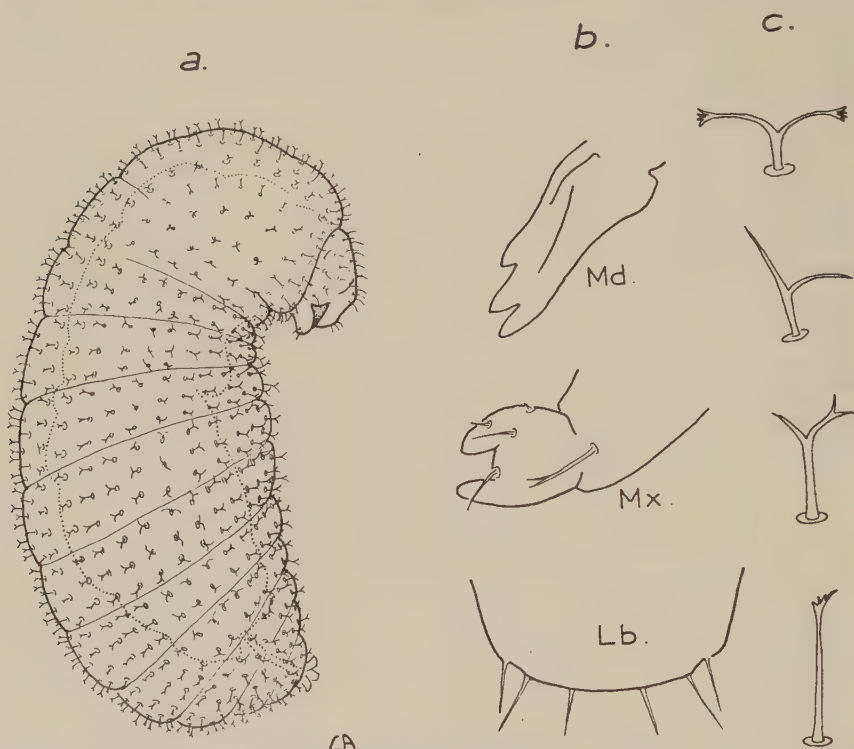


Fig. 2. — *Epixenus algericus* n. sp. : larve de 1^{mm},2 probablement au deuxième stade. — a, larve de profil ; on remarquera l'uniformité des poils et la séparation des segments, bien plus nette que chez *Monomorium* ; b, pièces buccales, $\times 200$. Les mandibules sont jaune foncé, les autres pièces incolores et munies de poils simples ; c, les quatre principales formes de poils du corps, $\times 250$. Ils sont presque tous bifurqués. Le deuxième type, à partir du haut, à pointes non ramifiées ni dentées, est de loin le plus fréquent.

peu distinctes sur la face dorsale et très difficiles à voir ventralement. Les dix segments abdominaux ont leurs séparations bien nettes dorsalement et ventralement, mais non prolongées sur les côtés, sauf à la bordure du pygidium.

Tous les segments et la tête portent de nombreux poils courts, dressés et plus ou moins incurvés. Seule la région des pièces buccales est peu poilue, avec quelques poils isolés rectilignes trois fois plus courts que les autres. Presque tous les poils du corps et du dessus de la tête sont courts, bifurqués,

à branches de la fourche incurvées. Cela rappelle beaucoup *M. salomonis*, mais, chez ce dernier, il y a en plus un cercle de grands poils, rectilignes, en avant du prothorax.

Ainsi faites, ces larves diffèrent notablement de celles des *Monomorium* déjà connus (*M. salomonis* (L.) et *gracillimum* Sm.) par leur corps moins cylindrique, bien plus poilu, les limites des segments beaucoup mieux indiquées, surtout pour les segments abdominaux 4 à 10. Le bord antérieur du prothorax ne porte pas de couronne de grands poils comme chez *Monomorium*.

Les types larvaires les plus voisins seraient ceux de *Leptothorax acervorum* Nyl., décrit par H. GANTÉS (1949, fig. 6, pl. V), et de *Pheidole dentata* Mayr, figuré par G. C. WHEELER (1953, fig. 11, pl. III). Encore ce *Pheidole* et ce *Leptothorax* ont-ils des poils larvaires plus longs et plus variés que notre *Epixenus*.

En somme, la larve d'*E. algiricus* est moins évoluée, moins simplifiée extérieurement que celles des *Monomorium*, ce qui correspond aux caractères des adultes, où la reine surtout est moins comprimée et moins différente des ouvrières que chez *Monomorium*. Le genre *Epixenus* est donc, à divers égards, plus primitif que son proche parent *Monomorium*. Si les ouvrières amènent à le rapprocher étroitement de *Monomorium*, les larves s'éloignent de la tribu des *Solenopsidini* et peuvent être comparées à celles des *Leptothoracini*, sauf pour la pilosité.

3° NOTES SUR LE COMPORTEMENT DES *EPIXENUS*

La première forme décrite, *E. andrei* Em., est basée sur des ♀ mêlées à un nid complet de *M. venustum* Sm., en Palestine. C'est tout ce qu'on en sait, et ce détail, joint aux pétioles dilatés, faisait considérer par EMERY les *Epixenus* comme des Fourmis parasites, très probablement dépourvues d'ouvrières.

Cette question est entièrement à reconsidérer depuis la découverte à Alger de nombreux nids pleins d'ouvrières normales, non mélangés à des fourmilères d'autres espèces. Nos observations, faites surtout en avril 1945 et en mai 1955, sont résumées ici et devront être complétées plus tard :

ÉCOLOGIE :

Aux environs d'Alger, *Epixenus algiricus* habite surtout l'argile pure, où il creuse des nids étroits, simples, peu profonds. Ces nids sont assez rares sur les collines à Lentisques (Kaddous, Ben Aknoun), relativement communs en forêt de Bainem, boisée de Pins d'Alep et située de 300 à 400 mètres d'altitude, près de la Méditerranée, à 6 kilomètres d'Alger. A Bainem, les ter-rains étudiés sont horizontaux ou presque. L'argile, jaunâtre, est très mêlée de gravier (quartz et gneiss) et se trouvait presque sèche lors du relevé

suivant, qui donnera une notion moyenne de l'habitat et des principales Fourmis concurrentes :

Relevé n° 147. — Route forestière allant de la forêt de Bainem à Guyotville. 12 mai 1955. Les fourmilières logent surtout dans l'argile dénudée des bords de la route, larges de 1 à 2 mètres. Plantes dominantes sur ces bords : *Trifolium* et *Asphodèles* ; dans la forêt : *Cistes* et *Quercus coccifera*. La rareté des Mollusques, des *Lampyris* et des *Cloportes* montre que cette station est relativement sèche, d'ailleurs loin de toute mare.

Voici, par ordre d'abondance décroissante, les nombres de nids des principales Fourmis, pour un total de 100 fourmilières repérées :

Tetramorium punicum (Sm.) : 18. — *Tapinoma simrothi* Krausse : 14. — *Epixenus algiricus* Bernard : 12. — *Cataglyphis viatica* Först. : 12. — *Messor barbara* (L.) : 10. — *Aphænogaster gemella* (Rog.) : 8. — *Camponotus barbaricus* (Em.) : 8.

Donc, ici, *Epixenus* vient au troisième rang par ordre d'abondance, et ses nids sont aussi fréquents que ceux de *Cataglyphis viatica*, espèce très banale sur ces sols argileux à Bainem, à Tunis et au Maroc. Ces Fourmis seraient sans doute encore plus abondantes si elles n'étaient concurrencées sur place par *Tapinoma simrothi*, importé d'Orient et très nuisible aux jardins d'Algérie.

Epixenus semble surtout insectivore, comme *Monomorium salomonis*, mais certains nids contenaient des débris de feuilles et de pétales de Ciste. Une ouvrière transportait un Hémiptère Capside tué.

STRUCTURE DES NIDS :

Les 24 fourmilières d'*E. algiricus* déjà explorées sont d'un type assez uniforme. Chacune s'ouvre à la surface de l'argile par un petit trou de 1 à 3 millimètres, peu visible. 1 à 2 centimètres après ce trou, on trouve déjà des larves, assez dispersées et non classées par rang de taille. Au plus 2 ou 3 courtes galeries divergentes, ne descendant guère qu'à 5 centimètres sous l'ouverture, contiennent reines, ouvrières et d'autres larves. Un nid à Kadous contenait au moins 8 reines ; les autres, probablement une reine ou 2 au maximum. Mais les ouvrières étaient toujours nombreuses, souvent plus de 500, et une fois plusieurs milliers.

L'allure et la vitesse des ouvrières sont très analogues à celles de *M. salomonis*. Les reines sont moins craintives et beaucoup moins cachées que chez la majorité des Fourmis locales. Malgré l'éventration du nid, plusieurs reines se promenaient au soleil dans le trou pratiqué et ne descendaient pas dans les galeries. Ce comportement indifférent caractérise aussi d'autres reines d'espèces polygynes, comme les *Monomorium* et les *Tapinoma*.

LESTOBIOSE ÉVENTUELLE :

Sur 24 nids d'*Epixenus* bien fouillés, il y en avait au moins 18 (75 %) entièrement indépendants, isolés à plus de 2 mètres de toute autre four-

milière et ne communiquant pas avec elle. 6 autres nids (25 %) étaient exactement au-dessus d'une fourmilière plus grande, avec mélange partiel des ♀ des 2 espèces :

- 2 avec *Messor barbara* (L.) ;
- 1 avec *Messor sancta* (Forel) ;
- 2 avec *Camponotus sylvaticus barbaricus* Em ;
- 1 avec *Monomorium salomonis* (L.), à Kaddous.

Dans ces cas de mélange, le nid superficiel d'*Epixenus* ne contenait aucune larve et le couvain était peut-être mêlé à celui de l'hôte ? Je n'ai pourtant pas réussi à distinguer de petites larves d'*Epixenus* parmi celles, 2 à 3 fois plus grosses, des *Messor* et *Camponotus*.

De tels nids directement superposés, avec mélange plus ou moins net des populations, rappellent d'autres espèces considérées comme « lestobiotiques » ou voleuses. Telles sont, en Europe, la plupart des *Solenopsis*. Il ne faut toutefois pas exagérer les habitudes pilleuses ou inquilines de ces minuscules Fourmis. FOREL les considérait comme toujours mêlées à d'autres genres, mais aussi bien à Banyuls (pour *Solenopsis Emeryi banyulensis*) que dans les Alpes (pour *S. monticola* Bernard), j'ai noté de nombreux nids homogènes, richement peuplés et fort éloignés de toute autre fourmilière. Dans les Alpes-Maritimes, *S. nicæensis* Bernard est tantôt associé à *Camponotus æthiops* Latr., tantôt manifestement indépendant. De même, les petits *Plagiolepis* (3 espèces en France et 5 en Afrique du Nord) sont souvent indépendants, parfois mêlés à de gros nids de *Camponotus* dont les habitants semblent indifférents à leur hôte de faible taille. Par contre, les Fourmis de dimensions plus réduites (*Pheidole*, *Monomorium*, *Tetramorium*...) perçoivent fort bien les *Plagiolepis* et *Solenopsis* et cherchent généralement à s'en débarrasser.

En résumé, *Epixenus algiricus*, comme bien des *Solenopsis*, forme très souvent des nids indépendants. Quand il est mélangé avec d'autres Fourmis, sans doute pille-t-il plus ou moins leur société, mais il ne semble pas très nuisible et la reine comme les larves de l'hôte ont alors une allure normale.

TABLEAU DES *Epixenus* DÉJÀ DÉCRITS :

Les 2 premières espèces : *E. andrei* Em. et *E. biroi* Forel ne sont établies que sur des ♀. J'y ajouterai la reine d'*E. algiricus* et donnerai un autre tableau pour les 2 ouvrières connues, d'ailleurs bien différentes l'une de l'autre. Le ♂ (*E. creticus* Em.) est encore trop douteux pour en tenir compte ici.

TABLEAU DES FEMELLES :

(Les 3 formes signalées se ressemblent beaucoup quant à la structure des antennes et des pétioles, qui, par conséquent, ne seront pas utilisés.)

1. Reine très lisse et très luisante, à pilosité jaune roussâtre. Dents postérieures de l'épinotum très larges, saillantes. Le mésonotum, étroit, rappelle celui de femelles ergatomorphes. Roux brun, 3mm,5 à 4mm,2. Crête, avec *Monomorium* *E. biroi* Forel.
- Reines en partie ponctuées ou réticulées, à pilosité blanchâtre. Dents de l'épinotum nettes, mais arrondies et peu saillantes. Mésonotum normal 2
2. Tête plus large que longue. Épinotum mat, très ponctué. 4mm,3, rousse. Palestine, avec *Monomorium venustum* *E. andrei* Em.
- Tête subcarrée. Épinotum assez luisant, réticulé. 3mm,8 à 4mm,1, brun foncé ou noire. Environs d'Alger, libre ou voisin d'autres Fourmis... *E. algiricus* Bernard.

TABLEAU DES OUVRIÈRES :

- Taille 2mm,2 à 2mm,5. Brun noir, appendices roux. Deuxième article du funicule égal à 3 et 4, tous à peine plus larges que longs. Mésonotum peu convexe. Épinotum sans dents nettes *E. algiricus* Bernard.
- Taille 1mm,8 à 1mm,9. Noires à appendices jaunes. Deuxième article du funicule très court, plus que 3 et 4, qui sont bien plus larges que longs. Mésonotum très convexe. Dents postérieures de l'épinotum très visibles..... *E. guineensis* Bernard, monts Nimba (Guinée).

Résumé.

Les petites Fourmis du genre *Epixenus*, considérées comme parasites et sans ♀ par EMERY (1922), sont en réalité souvent pourvues d'♀ nombreuses et capables de nicher indépendamment. C'est le cas d'*E. algiricus* Bernard, décrit ci-dessus, qui peut avoir plus de 1 000 ouvrières et 8 reines. Le quart seulement des nids observés aux environs d'Alger semblaient associés à d'autres genres, surtout *Messor* et *Camponotus*. Les *Epixenus* (4 espèces certaines) sont surtout insectivores et assez proches des *Monomorium*, avec toutefois des larves et des reines plus primitives.

Summary.

The small Ants of the genus *Epixenus*, described by EMERY (1908) as probably parasitic and without workers, are in fact often with numerous workers and have independent nests. The best known is *E. algiricus* Ber-

nard, described here, having sometimes more than 1 000 ♀ and 8 queens. Only one fourth of the nests observed in the neighbourhood of Algiers seems to be associated with other genera, chiefly *Messor* and *Camponotus*. *Epixenus* (4 sure species) are mainly insectivorous and near *Monomorium*, with, however, queens and larvae more primitives.

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CONTRIBUTION A L'ÉTUDE BIOLOGIQUE DES POLISTES (HYMÉNOPTÈRES VESPIDES) II. — LE CYCLE ÉVOLUTIF DU COUVAIN

par

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A. — GÉNÉRALITÉS

L'évolution naturelle du couvain chez *Polistes* présente une alternance caractéristique de deux phases successives que nous avons appelées phase du couvain « normal » et phase du couvain « abortif » (DELEURANCE, 1952 a). Au cours de la première, les larves se développent rapidement et donnent naissance à des imago sains ; dans la deuxième, leur croissance se ralentit ; elles avortent en majorité ou produisent des imago anormaux.

Notre exposé vise à mettre au point les données actuellement recueillies sur cette importante question, qui, par certains côtés, reste encore obscure.

Afin d'avoir une vue d'ensemble du problème et pour en dégager les données essentielles, observons en détail l'évolution du couvain dans le cas d'une jeune fondatrice

Position chronologique.		1	2	3	4	5	6	7	8	9	10 _a	10 _b	12 _a	12 _b	14 _a
Vie larvaire (jours).	♀ normales.	16	15	16	16	18	17	18	19	21					
	♀ anormales.											26		26	
Vie larvaire (jours) (→ mort ou expulsion).	Larves abortives.										35		25		34
« Stade larvaire ».											L+		L+		L+

P. gallicus (élevage au laboratoire).

TABLEAU N° 2.

Durées comparées de la vie larvaire du vieux couvain « repris » par les ♀ (a) et du jeune couvain nourri dès sa naissance par les ♀ (b).

a

Age des larves.	22	22	20	20	16	9	7	6	6	6
Vie larvaire.	28	28	26	27	26	22	21	18	19	18

b

Position chronologique.	1	2	3	4	5	6	7	8	9
Vie larvaire.	18	16	17	18	19	20	22	23	22

N. B. — Dans le tableau a, nous ne considérons que les vieilles larves qui ont évolué normalement.

La durée moyenne de la vie larvaire pour la couvée élevée uniquement par la fondatrice fut de seize jours.

P. gallicus (élevage au laboratoire).

absence d'♂.

17 _a	17 _b	19	20	21	22	23 _a	23 _b	25 _a	25 _b	27	28	29	30	31	32	33
35	35	32	31	31	30	29	29	28	28	26	15	10	10	9	10	5
L+	L+	L+	L+	L+	L+	L+	L+	L+	L+	L+	JL	JL	JL	JL	JL	E

dont la première couvée est dépourvue d'ouvrières (tableau 1). On constate que les neuf premières larves se développent normalement et donnent des imago sains. Puis les suivantes avortent ou produisent des femelles anormales. Enfin, l'avortement au stade larvaire se généralise et frappe tout le couvain. Parallèlement à cette évolution, on remarque deux choses :

a. Le ralentissement progressif de la croissance larvaire.

b. La mort ou l'élimination des larves abortives se fait tout d'abord à un âge de plus en plus avancé ; puis le phénomène s'inverse : les larves « avortent » à un stade de plus en plus précoce. Dans le cas extrême, la Guêpe n'élève même plus la larve qui vient d'éclore.

Le caractère de cette évolution suggère que la cause du couvain abortif doit être de nature trophique. La capacité nutritive de la jeune fondatrice ne lui permet d'élever qu'une seule couvée. Normalement, les ouvrières assurent, sans doute, le relais trophique dans la société. Effectivement, on constate (tableau 2, *a*) alors qu'après une phase couvain « abortif » plus ou moins prononcée les ouvrières nourrices rétablissent l'évolution normale des larves. L'examen du tableau 2, *a* montre, en outre, que, plus le couvain repris par les ouvrières est jeune, plus son développement est rapide. Lorsque, à leur tour, les ouvrières déclinent, le couvain périclité à nouveau et redevient abortif. Si elles ne sont pas relayées par de jeunes sœurs, l'avortement des larves est général (le phénomène évolue d'une manière absolument identique à celle que nous avons représentée dans le tableau 1 précédent). Ceci peut être démontré par l'expérience : il suffit de procéder au « rajeunissement » de la population. La figure 8 schématise les résultats obtenus en remplaçant deux fois par une jeune Guêpe le vieux sujet.

Cette exploration préliminaire nous a conduit à rechercher l'explication des phases couvain « normal » et couvain « abortif » dans l'analyse des conditions de l'alimentation des larves par les adultes.

B. — ÉTUDE DU NOURRISSEMENT DES LARVES PAR LES ADULTES

a. **Étude quantitative.** — Lorsqu'un couvain devient abortif, l'apport de proies par les Guêpes diminue corrélativement (1). On peut se demander si l'avortement des larves ne résulte pas d'une alimentation protéinique

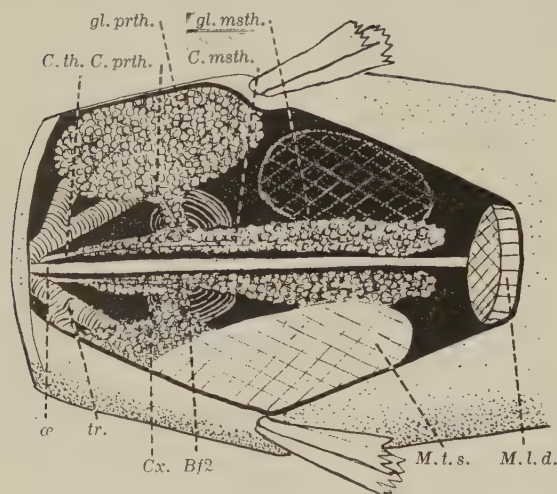


Fig. 1 a.

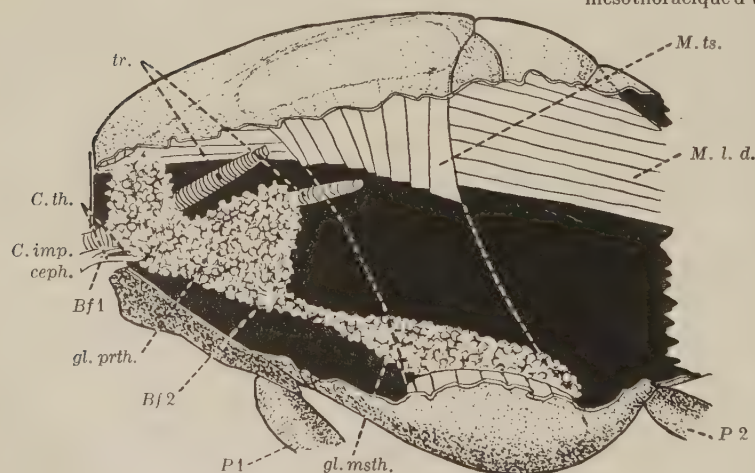


Fig. 1 b.

Fig. 1. — a, schéma montrant la glande labiale *in situ*; vue en plan. Une fenêtre a été pratiquée sur la face tergale. On distingue l'insertion sur le plancher mésosternal du muscle tergosternal droit (enlevé). Le muscle longitudinal dorsal a été sectionné. — b, Schéma montrant la glande labiale *in situ*; vue de profil. Le thorax est ouvert latéralement et une portion du muscle tergosternal gauche enlevée.

Bf 1, bifurcation primaire du canal salivaire; Bf 2, bifurcation secondaire; C. imp. ceph., canal impair céphalique; C. msth., canal de la glande labiale mésothoracique; C. prth., canal de la glande labiale prothoracique; C. th., canalsalivaire thoracique, collecteur commun des glandes labiales prothoracique et mésothoracique d'un même côté; Cx,

coxa; gl. msth., massif glandulaire labial mésothoracique; gl. prth., massif glandulaire labial prothoracique; Lb., labium; M. l. d., muscle longitudinal dorsal; M. t. s., muscle tergosternal; Œ., œsophage; p1, patte antérieure; p2, patte intermédiaire; tr., tronc trachéen. (D'après RABATÉ.)

insuffisante. L'expérience paraît répondre négativement. En effet : 1° un couvain sous-alimenté, de jeunes Guêpes (par rationnement des adultes), évolue normalement. Les imago produits sont petits, mais sains. En outre,

(1) En élevage, le retard dans la récolte des proies avertit l'observateur de l'imminence de la phase abortive.

il suffit de cesser le rationnement pour rétablir les conditions habituelles du développement larvaire (1). — 2° Au contraire, la vieille Guêpe qui donne un couvain abortif peut être artificiellement gavée sans que le destin des larves soit changé. Ces expériences montrent, par ailleurs, que la diminution, puis l'arrêt des apports de proies sont un *effet* du couvain abortif. Car, d'une part, plus les larves deviennent anormales, plus la Guêpe

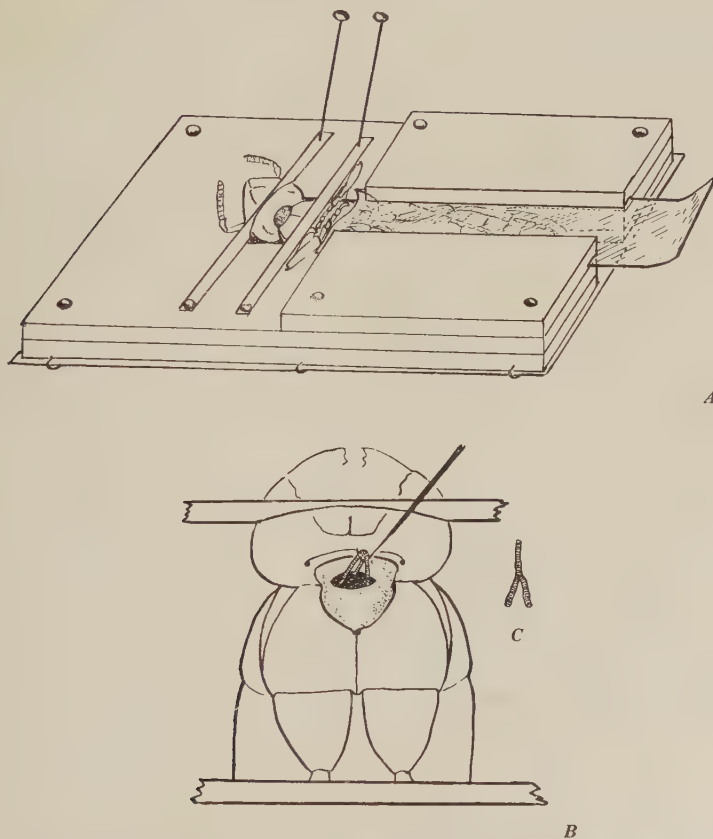


Fig. 2. — A, disposition opératoire. — B, extraction du canal salivaire à l'aide d'un micro-crochet, après ouverture d'une boutonnière dans le cou. — C, portion du canal réséquée. (D'après RABATÉ.)

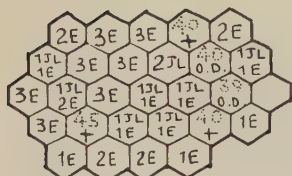
répugne à accepter les proies qu'on lui présente (et à nourrir). Et, d'autre part, si l'on substitue un couvain abortif à un couvain normal, les jeunes Guêpes diminuent immédiatement leur récolte de proies.

Avant de conclure, un dernier point méritait examen. La couvée, chez le Poliste, n'est pas nourrie anarchiquement. L'alimentation est donnée selon un certain « ordre ». Les larves âgées sont nourries en priorité ; les dernières servies sont les plus jeunes, lesquelles, normalement, occupent, dans le nid, une position périphérique. On peut supposer que ce phé-

(1) TURNER (1912) a constaté qu'un jeûne prolongé n'avait pas de conséquences fatales pour le couvain.

nomène soit à l'origine de l'avortement des dernières larves de la première couvée, par exemple. Sans rejeter toute influence possible du « gradient » d'alimentation, il est cependant facile de démontrer qu'il reste étranger à la question qui nous occupe. En effet, à l'arrivée de la phase abortive, éliminons

Nid 13-52



Nid 11-52



Nid 15-52



Nid 10-52

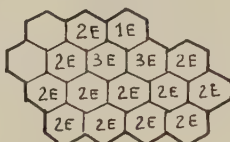


Fig. 3. — Représentation schématique de l'évolution du couvain pour les quatre nids dont la population a subi la résection des canaux salivaires (cf. tableau 3).

E, larves mortes aux tout premiers stades. — J L, larves mortes à l'état de jeunes larves (larves latérales). — +, larves mortes au dernier stade et n'ayant pas filé d'opercule. — O D, opercules détruits par les adultes (les larves abortives sont expulsées).

Les chiffres en pointillé indiquent la durée de la vie larvaire.

Les chiffres pleins indiquent le nombre de larves qui se sont succédé dans chaque alvéole. (D'après RABATÉ.)

se tarirait avec l'âge (1). Ceci nous amena à rechercher des indications dans ce sens en étudiant particulièrement le rôle des glandes salivaires (glandes labiales).

A première vue, l'intervention de facteurs oligodynamiques se présente favorablement. Si, par exemple, on adjoint une jeune nourrice à une vieille Guêpe en s'arrangeant pour que la vieille Guêpe soit l'*unique* récolteuse de proies, la couvée produite est normale. Signalons également que les essais de nourrissage *direct* des larves se soldent par un échec.

Un moyen radical d'éprouver le rôle éventuel des sécrétions salivaires dans le nourrissage des larves consistait à les supprimer. L'ablation des glandes labiales, logées dans le thorax (fig. 1, a et b) s'avérant trop problématique, nous avons tourné la difficulté en procédant à la résection,

ces dernières larves, ou mieux donnons aux Guêpes un autre nid : la nouvelle couvée produite sera *totale*ment abortive.

Ces résultats nous ont conduit à rechercher la cause de l'avortement des larves dans la qualité de la nourriture servie.

b. Étude qualitative.

— L'hypothèse d'un simple déséquilibre dans la *ration* alimentaire (notamment pour les substances protéiniques et glucidiques) ne semble pas devoir être retenue : l'observation ne décèle rien d'exceptionnel. Nous avons donc pensé à l'existence possible de substances oligodynamiques produites par les Guêpes nourries, dont la source

(1) Ou l'épuisement.

TABLEAU N° 3.

NOMBRE de Polistes par nid.	Nids.	NOMBRE de cellules par nid.	NOMBRE de larves écloses.	Destinée des larves écloses.						DÉSOPERCULATIONS.		NOMBRE d'imag.
				NOMBRE de ces larves mortes aux tout premiers stades.	NOMBRE de ces larves mortes à l'état de jeunes larves.	LARVES AVORTANT au dernier stade et incapables de filer.		LARVES AYANT filé un opercule.		Nombre. Nombre de jours après l'oper- culation.		
						Nombre.	Age à l'avorte- ment.	Nombre.	Durée de la vie larvaire.			
3	13-52	28	54	40, soit 74 %	9, soit 64 % des larves restantes.	3, soit 5 à 6 %	40-40 et 45 jours.	2	39 et 40 jours.	2	1 et 5 jours.	0
1	11-52	14	26	26, soit 100 %	0	0		0		0		0
4	15-52	16	32	24, soit 75 %	4, soit 50 % des larves restantes.	1, soit 3 %	40 jours.	3	34-41 et 45 jours.	3	0-6 et 11 jours.	0
3	10-52	17	31	31 soit. 100 %	0	0		0		0		0
Nid témoin monogyne 1 ^{re} couvée (phase cuvain normal).		30	10	0	0	0		10	18 jours en moyenne.	0		10

sur une grande longueur, du canal salivaire impair, près du point de jonction des deux canaux latéraux (fig. 2, A et B). Les résultats de ces expériences exécutées par RABATÉ (1954) et nous-même sur *P. nimpha* et *P. gallicus* se sont révélés très significatifs. Toutes les larves, élevées depuis leur

naissance par les Guêpes ainsi traitées, avortèrent (fig. 3). De plus, la lenteur de leur croissance et leur évolution les apparentent étroitement au couvain abortif naturel (tableau 3) (1).

Une étude anatomique et histologique fut alors effectuée par RABATÉ, dont le but était notamment de rechercher s'il n'existait pas un parallélisme entre l'évolution de ces glandes et celle du couvain. Cet auteur a constaté que ces organes avaient anatomiquement un développement important. Chaque glande se décompose en deux massifs, l'un (fig. 1 et 4, *g. prth.*) occupe une position antéro-latérale, l'autre une position longitudinale et ventrale (*g. msth.*). La glande, du type en grappe, est formée de lobules sphériques (diamètre 80 μ). La structure de ces lobules fut incorrectement interprétée par LEYDIG (1858), puis BORDAS (1894), chez *Vespa* (2).

Un traitement à la potasse montre (fig. 5) que le canal efférent qui sort du lobule s'arboresce à l'intérieur en fins canalicules, ramifiés à leur tour et terminés en cul-de-sac ; leur structure rappelle les trachéoles terminaux des cellules trachéennes. L'étude histologique indique qu'ils sont intracellulaires (fig. 6). L'examen sur coupe (fig. 6) permet de se rendre compte de la structure du lobule.

A la périphérie, encapsulant une cellule centrale géante, on observe une assise de cellules (*c. p.*) bordées par une membrane basilaire externe. Sur une section équatoriale, on en compte en moyenne sept à huit. La cellule centrale (*C. c.*) contient un gros noyau de forme irrégulière possédant de nombreux nucléoles. Les canalicules terminaux pénètrent son cytoplasme et se distribuent sur son pourtour (3). Cette structure complexe et le développement des glandes salivaires soulignent sans doute l'importance de leur rôle. Mais leur sécrétion est-elle en rapport avec le développement normal du couvain ? RABATÉ pense

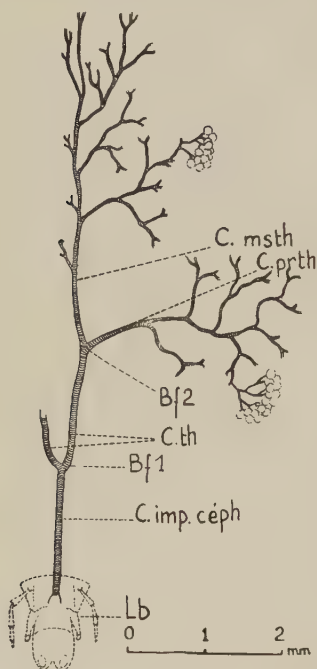


Fig. 4. — Disposition semi-schématique des canaux salivaires de la glande labiale. Seuls figurent les canaux correspondants de la glande gauche. Quelques lobules glandulaires ont été esquissés. (D'après RABATÉ.) (Pour la légende cf. fig. 2.)

(1) Du type *sec* (cf. plus loin).

(2) Elle est la même que chez *Polistes* (RABATÉ).

(3) Cette cellule géante à noyau irrégulier avec canalicules intracellulaires rappelle les cellules des glandes pharyngiennes observées par N. B. PALM chez *Bombus* (1949).

en trouver la confirmation histologique dans leur évolution. L'aspect des lobules glandulaires chez les Guêpes, qui produisent du couvain abortif indique une dégénérescence cellulaire (fig. 7). En fait, nous ne sommes pas absolument convaincu par les images histologiques qu'il nous présente. Il est, par ailleurs, possible que les glandes salivaires aient des fonctions multiples. Pour l'instant, nous nous contenterons seulement d'une présomption.

Au terme de cette étude générale sur l'influence de la nutrition dans l'évolution abortive des larves, nous pouvons émettre l'hypothèse suivante : l'apparition du couvain abortif est liée à une carence alimentaire de nature qualitative. La Guêpe donne aux larves des substances oligodynamiques indispensables à leur développement normal. En vieillissant, elle devient incapable de fournir ces substances, et les larves avortent. Les glandes labiales représenteraient la source de ces facteurs oligodynamiques.

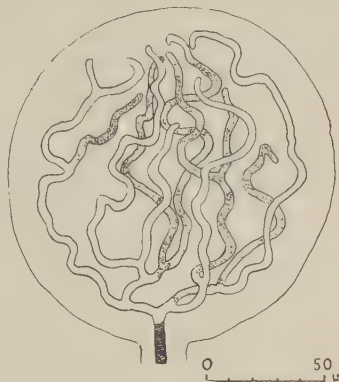


Fig. 5. — Canalicules intracellulaires d'un lobule de la glande labiale de *Polistes gallicus*, après traitement à la potasse. (D'après RABATÉ.)

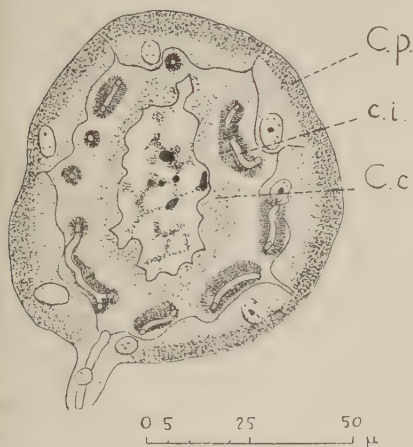


Fig. 6. — Lobule glandulaire de *Polistes gallicus* jeune en activité. Coupe histologique équatoriale. C. p., cellules périphériques ; c. i., canalicules intracellulaires ; C. c., cellule centrale. (D'après RABATÉ.)

On constatera que, dans l'ensemble, cette explication apparaît satisfaisante, notamment, si l'on se souvient (tableau 1) du caractère très progressif de l'évolution abortive et de l'existence d'un point critique d'irréversibilité dans les effets de la carence alimentaire.

C. — LES EFFETS DU COUVAIN ABORTIF SUR L'ÉVOLUTION DES COUVÉES. LES FACTEURS MICROBIENS

Si l'hypothèse précédente est exacte, on doit pouvoir en administrer la preuve de la manière suivante. En remplaçant périodiquement par des jeunes Guêpes les vieilles nourrices, on doit réaliser un guépier « pérenne ». L'expérience réalisée au laboratoire s'est révélée significative (fig. 8). Mais nous avons constaté que les résultats n'étaient pas parfaits. La phase couvain « abortif » tend à prédominer, phénomène que révèlent, d'une part, l'augmentation de la proportion des imago anormaux, et, d'autre part, l'allongement de la durée de

la vie larvaire (tableau 2, *a* et *b*). Nous en avons recherché les raisons.

a. Effet du couvain abortif sur les imago. — Nous nous sommes aperçu que le couvain abortif laisse des traces tenaces de son passage sur

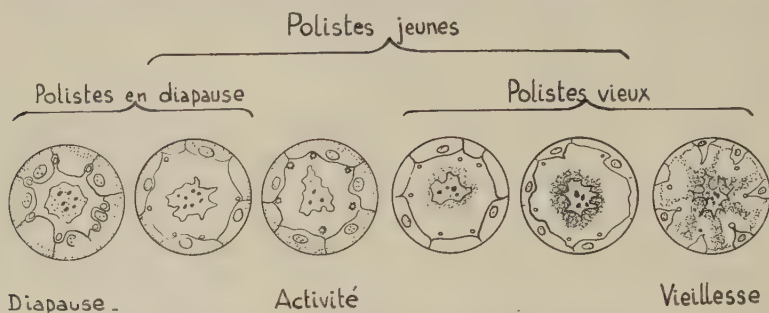


Fig. 7. — Représentation schématique de l'évolution d'un lobule glandulaire. (D'après RABATÉ.)

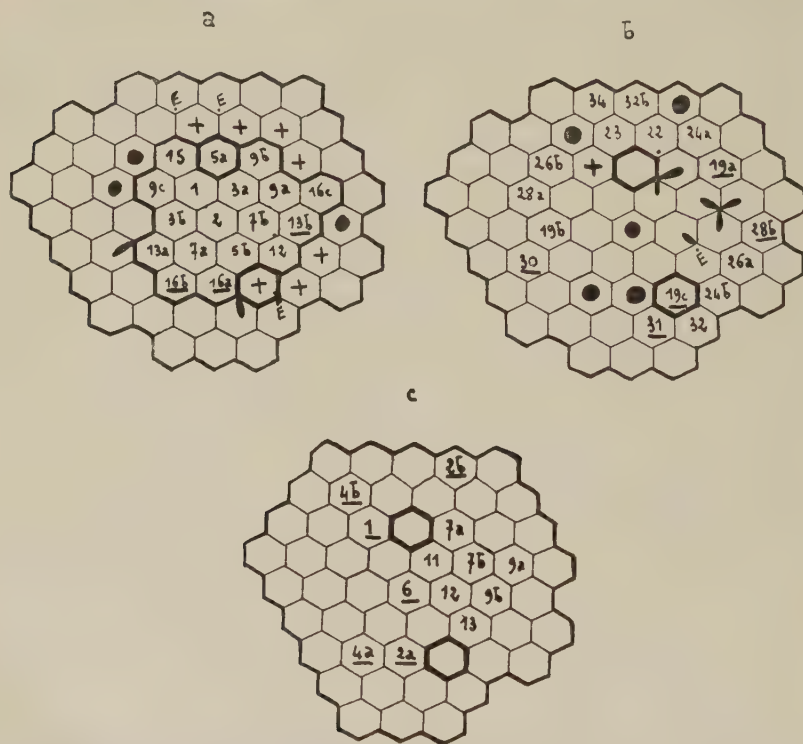


Fig. 8. — *a*, couvain larvaire du nid lors du premier changement de la Guêpe. — *b*, couvain larvaire du nid lors du deuxième changement de la Guêpe. — *c*, évolution du couvain repris par la jeune Guêpe en *b*.

+, larve axiale âgée ; ●, larve axiale jeune ; /, larve latérale ; E, larve venant d'éclore.

Les chiffres indiquent : en *a*, la position chronologique des larves intégralement élevées par la première fondatrice ; en *b*, la position chronologique des larves suivantes, élevées par la deuxième femelle ; en *c*, l'ordre des larves restantes en *b* suivant l'âge (la larve la plus âgée prenant le n° 1).

Les chiffres soulignés indiquent les larves qui ont avorté (couvain abortif) ; les chiffres non soulignés donnent le couvain normal.

les nids. Nous savions (DELEURANCE, 1950) qu'il déclenche le phénomène connu sous le nom de « massacre du couvain », à l'automne. Mais nous ignorions ses effets persistants. Or les larves abortives (surtout par leur défécation lors de l'entrée en nymphose) imprègnent le nid d'une odeur tenace (perceptible) qui perturbe le comportement normal des Guêpes. Il s'ensuit que les larves, mal nourries, tendent à devenir chroniquement abortives. Nous avons pu mettre ce phénomène en évidence de plusieurs manières :

1° Si l'on fait adopter un vieux nid ayant contenu du couvain abortif par de jeunes femelles, les larves évoluent anormalement. La proportion des imago sains reste faible et la société périclité.

2° On peut reproduire dans une large mesure les mêmes phénomènes sur un nid sain en déposant simplement avec un pinceau un extrait alcoolique de larves abortives sur le gâteau.

3° Si, au lieu de rajeunir la population d'un vieux nid, on transfère le couvain sur un nid sain, la proportion des larves évoluant normalement devient beaucoup plus considérable.

4° Enfin, en désodorisant les nids, on observe une amélioration sensible dans l'évolution du couvain. Ainsi, en couplant les renouvellements de population avec la désodorisation, nous sommes parvenu à maintenir pendant huit mois un nid à peu près normal.

Ces faits nous indiquent que la société « pérenne » est difficilement réalisable avec *Polistes*. Ils contribuent à expliquer comment, même dans les régions tropicales, le nid reste saisonnier.

b. Les facteurs microbiens. — Nos essais sur la « pérennité » expérimentale des nids de *Polistes* nous ont conduit à la découverte d'un autre facteur dans le phénomène du couvain abortif. Celui-ci, de nature bactérienne, s'est également révélé défavorable à la persistance des sociétés. Il s'agit d'un agent pathogène du genre *Serratia* (VERGÉ, 1952). Il semble que les larves carencées deviennent les victimes d'une infection qui se généralise à tout le couvain, même sain. En effet, si l'on sert à celui-ci des larves contaminées réduites en bouillie, il devient à son tour abortif. De même, des *Serratia* cultivées sur milieu gélosé et administrées par voie buccale à des larves saines provoquent rapidement leur mort. Lorsque cette maladie atteint le couvain d'un nid, les rajeunissements de population deviennent inopérants : le couvain devient chroniquement abortif. Nous avons néanmoins réussi, à l'aide d'antibiotiques, à maîtriser cette infection. Certaines années, elle est très répandue à la fin de la belle saison.

Quand les larves abortives d'origine purement trophique meurent, elles se racornissent et se dessèchent sur place, en prenant une teinte brique. Elles ne dégagent pas d'odeur appréciable. Nous avons là le couvain abortif du type *sec*. Au contraire, les larves qui succombent aux *Serratia* deviennent noirâtres et pourrissent en dégageant une forte odeur. Elles caractérisent le type abortif « loque ». Les Guêpes sont beaucoup plus sensibles à la « loque » qu'au couvain abortif *sec*.

En définitive, la connaissance des effets du couvain abortif sur les Guêpes permet d'expliquer nos échecs relatifs quant à la réalisation de nids « pérennes ». Par là même, elle tend à confirmer notre point de vue sur la cause originelle (de nature trophique) de l'évolution alternée des phases couvain « normal » et couvain « abortif ».

D. — EFFETS DE LA NATURE DES PROIES SUR LE COUVAIN

Nous pensions avoir ainsi à peu près résolu le problème, lorsque notre attention fut attirée sur un autre point. Dans nos élevages, les Guêpes disposent, surtout pendant la saison froide, de jeunes Grillons (*G. domesticus*). Or, quand les Polistes utilisent des Grillons comme source *unique* d'aliments protéiniques, le nombre des Guêpes filles (ou fils) produites est nettement inférieur à la moyenne. En outre, la phase couvain « normal » est écourtée. La société disparaît précocement : on n'obtient jamais de grands nids.

Nous nous sommes demandé si le régime *monophagique* de ces élevages n'était pas à l'origine d'une carence alimentaire qui troublerait l'évolution normale du couvain. En 1954, nous avons donc éprouvé l'influence éventuelle du régime monophagique sur le couvain en donnant aux Guêpes *uniquement* des chenilles de Ver à soie (*B. mori*). Nous avons alors constaté que les fondatrices donnaient de splendides et populeuses sociétés ! La conclusion s'imposait : le régime monophagique n'est pas en cause, mais la *nature* des proies chassées revêt une grande importance pour le développement normal des larves.

L'ensemble de nos observations peut se résumer ainsi. 1^o Avec des Grillons, la fondatrice produit en moyenne sept imago sains. Le couvain abortif apparaît rapidement. Le relais du nourrissement par les ouvrières est imparfait : le retour à la phase couvain normal reste fugace. Souvent, avant même la production des mâles, le couvain avorte en totalité : la société est déjà condamnée. — 2^o Avec les Vers à soie, la fondatrice nous a donné en moyenne vingt-quatre imago. La première phase couvain abortif est à peine marquée. Le relais par les ouvrières s'effectue parfaitement. Les couvées se succèdent et la société évolue à la perfection. La phase abortive finale coïncide avec l'épuisement général de la population active.

Jusqu'ici, le fait de l'influence de la nature des proies sur le développement favorable des larves n'apparaît contradictoire ni avec les phénomènes précédemment observés, ni avec notre explication. Mais nos dernières expériences apportent des constatations nouvelles, qui, elles, paraissent difficilement conciliables avec l'hypothèse concernant l'action de facteurs oligodynamiques. Ces contradictions résultent des deux séries d'expériences suivantes :

1^o Soit une jeune fondatrice qui dispose uniquement de Grillons. Au moment où la phase couvain abortif apparaît, on remplace les Grillons par

des chenilles de Vers à soie. L'approvisionnement en proies reprend : le couvain se rétablit.

2° Si on introduit en cage d'élevage approvisionnée avec des Grillons une jeune fondatrice et son nid (récoltés dans la nature) dont la première couvée est déjà en partie operculée, le couvain abortif frappe presque immédiatement les larves restantes. Avec des Vers à soie, l'évolution reste normale.

Si l'on admet que le régime Grillons provoque une carence alimentaire chez la Guêpe nourrice, qui se manifeste en moyenne dès la huitième larve de la première couvée, on comprend mal qu'en donnant à ce moment des Vers à soie la Guêpe retrouve un régime équilibré qui lui permette de sécréter à nouveau les substances oligodynamiques indispensables au couvain. Car pourquoi alors la Guêpe de l'expérience 2, qui vient de la nature, donnera-t-elle presque immédiatement du couvain abortif ? Si la cause provient du régime Grillons, elle ne devrait apparaître chez cette fondatrice qu'aux environs de la huitième larve élevée *depuis* la mise en cage de la Guêpe avec son nid. Nous voyons là une contradiction avec notre hypothèse sur l'origine oligodynamique du couvain abortif (1), origine liée au vieillissement (ou à l'épuisement) de la Guêpe.

E. — DISCUSSION

On pourrait sans doute donner des expériences précédentes une explication très simple qui ferait intervenir le facteur alimentaire *quantitatif* dans l'origine du couvain abortif. Supposons qu'un facteur comme l'*appétit* soit en jeu (de fait, la Guêpe attaque beaucoup plus vigoureusement les Chenilles que les Grillons, et la fréquence des apports de proies augmente avec les premières). Lorsque la nourrice est jeune, sa motivation reproductrice est maximale : la nature de l'espèce chassée a peu d'influence sur son comportement (2). Les premières larves, correctement nourries, évoluent normalement. En vieillissant, la nourrice devient beaucoup plus sensible à la nature des proies. En conséquence, elle se rabat sur le gibier préféré. D'où les différences constatées entre les élevages disposant de Grillons et ceux pourvus de Chenilles. Le même phénomène se reproduirait avec les ouvrières. Le couvain abortif serait alors d'origine trophique, mais il s'agirait d'un trouble de nature quantitative ? Il serait en relation avec un phénomène banal de vieillissement : les larves périeraient de simple inanition ?

(1) Étant données les grandes variations dans la capacité nutritive des fondatrices, pour être certain de leurs résultats, les deux types d'expériences précédentes devraient être exécutés sur une échelle plus grande que celle adoptée. Néanmoins, les constatations nous ont paru suffisamment nettes pour en faire état.

(2) Dans la nature, le Poliste se montre très éclectique. Outre les Chenilles, il attaque : Diptères, Orthoptères, Hémiptères, etc. Nous l'avons même vu chasser des Opilions (*P. bimaculatus*) à Besse-en-Chandesse.

Une confrontation générale des données du problème s'impose pour essayer de faire le point.

En fait, on peut tenir pour acquise l'origine trophique du couvain abortif. Seule reste en suspens la question de savoir si sa cause fondamentale réside dans le tarissement avec l'âge des substances oligodynamiques sécrétées par la Guêpe nourrice, ou bien s'il s'agit simplement d'une insuffisance *quantitative* des aliments distribués par les Polistes âgés (1).

En faveur de la première hypothèse, nous avons les faits suivants : 1° les expériences sur la résection des canaux salivaires ; 2° à un moindre degré, les images histologiques des glandes labiales ; 3° l'échec du nourrissage direct des larves à l'aide de miel, d'eau et de proies malaxées ; 4° enfin, les expériences où une jeune Guêpe, *qui ne récolte pas* de proies, est adjointe à un vieux sujet (p. 290).

Contre cette hypothèse, nous avons les observations précédemment rapportées (D).

Allons-nous choisir l'une *ou* l'autre de ces deux hypothèses ? En l'état actuel de nos travaux, nous ne le ferons pas. Nous pensons que la première hypothèse a de la valeur ; elle mériterait d'être approfondie par de nouvelles recherches. Nous croyons qu'en fait le facteur *quantitatif* n'exclut pas le facteur *qualitatif*. L'avortement du couvain doit avoir des causes multiples, et nos dernières expériences montrent, semble-t-il, qu'une d'entre elles peut être d'ordre quantitatif, tout en étant liée à la nature des proies chassées. A cet égard, nous pensons que notre hypothèse relative à l'épuisement, chez la vieille nourrice, de substances oligodynamiques indispensables aux larves ne doit pas être abandonnée. Car, en définitive, avec les Polistes disposant de Chenilles, l'allure générale du phénomène ne change pas, même si, manifestement, la société évolue beaucoup mieux qu'avec les Grillons.

Nous signalerons pour terminer que le nourrissage normal des larves par les adultes pose des problèmes complexes qui mériteraient une étude approfondie. C'est ainsi qu'une différence de 15 à 20° entre les températures *moyennes* auxquelles sont soumises les larves et les adultes provoque la formation de couvées abortives. Nous l'avons constaté au cours d'expériences (conduites afin de rechercher le déterminisme des castes, DELEURANCE, 1952 *b*) où soit les adultes, soit les larves, passaient leur « nuit » à la glacière. Ceci prouve que, dans le développement normal, l'interdépendance entre le couvain et les adultes est très étroite.

F. — EFFETS ÉTHOLOGIQUES ET SOCIAUX DU COUVAIN ABORTIF

Nous terminerons cette étude par un bref examen des influences du couvain abortif sur la biologie des Polistes.

(1) L'alimentation glucidique n'entre sans doute pas en jeu, car les apports de miel ne fléchissent pas comme la récolte des proies.

a. *Caractère temporaire des sociétés de Polistes.* — Il est très probable que l'action répulsive du couvain abortif sur les adultes joue un rôle important dans l'absence de pérennité chez les sociétés de *Polistes*. Elle s'oppose à la conservation du nid. Le phénomène est particulièrement net au laboratoire. Nous l'avons constaté à Marseille, dans la nature, où des ouvrières de *P. omissus* abandonnaient leur nid d'origine, devenu « abortif », et passaient sur des nids étrangers.

b. *Valeur reproductrice des Guêpes filles.* — Il est également probable que les très grandes inégalités observées dans la valeur reproductrice des Guêpes filles tiennent pour une bonne part à l'évolution si particulière du couvain chez *Polistes*. Les meilleurs individus proviennent du centre des couvées. Nous avons pu nous en assurer au laboratoire.

c. *Caractères morphologiques des sujets anormaux.* — Parfois l'imago provenant d'une couvée abortive est d'apparence normale. On constate pourtant qu'il manque de vigueur. Il meurt toujours prématurément. Les malformations physiques les plus courantes affectent les membres : pattes tordues, ou écourtées ; tarses anormaux. Le brachyptérisme et l'aptérisme sont très fréquents. Notons que tous ces sujets anormaux sont l'objet d'une nette hostilité de la part de la société ; ils finissent généralement par être expulsés (1).

d. *Comportement des adultes.* — 1^o Lorsque la fondatrice, à la fin de sa vie solitaire, commence à donner du couvain abortif, son activité décroît : elle devient casanière. Elle donne à ce moment l'impression « d'attendre la venue des ouvrières pour repartir à l'action ». Certaines fondatrices, excellentes reproductrices, n'engendrent pratiquement pas de couvain abortif. En ce cas, leur activité *ne s'arrête pas*. Nous avons pu constater (dans la nature comme dans les élevages) que les fondatrices qui cessent de travailler *avant* l'apparition des ouvrières sont des Guêpes médiocres. Dans tous les cas, la société reste chétive et disparaît prématurément. On signalera ce phénomène indicatif : plus la Guêpe a cessé tôt de travailler, moins le nid se développera ultérieurement. Ceci s'explique par les séquelles de la phase couvain abortif. Pour l'observateur, la connaissance de ce détail éthologique revêt une grande importance.

La chute de l'activité générale, à l'operculation de la première couvée, peut avoir une autre cause. A ce moment, la deuxième couvée n'est composée que de jeunes larves, lesquelles ne déclenchent qu'une faible activité chez les adultes. Si l'activité reproductrice de la Guêpe est essentiellement due à la présence d'un couvain *actif*, on s'explique la chute observée dans le travail du sujet. Car le travail des fondatrices, à la fin de l'operculation de la première couvée, est en relation avec le deuxième cycle de la multiplication alvéolaire : il concerne presque exclusivement l'activité bâtisseuse

(1) Cette hostilité provient, sans doute, de leur odeur « abortive » et non pas, en général, de leur comportement.

d'origine « interne » (DELEURANCE, 1954). Les femelles à faible fécondité, qui construisent peu de nouvelles cellules, cessent donc pratiquement de travailler.

En fait, cette deuxième cause ne peut que s'additionner à la première, car la présence de couvain abortif retentit toujours d'une manière défavorable sur l'activité générale (1).

Dans la société, la présence de couvain abortif n'amène pas seulement le fléchissement de l'activité reproductrice des adultes, elle modifie les rapports sociaux. Selon nous, cette modification est en étroite corrélation avec l'augmentation de l'*irritabilité* chez les Guêpes. En polygynie (secondaire surtout), elle se traduit par une évolution caractéristique. La pondreuse principale (= femelle α de PARDI, 1946) devient nettement hostile envers ses compagnes ; il en résulte des bagarres parfois extrêmement violentes. Ainsi que l'a constaté l'auteur italien, cette intolérance s'exerce différenciellement ; la pondreuse principale importune beaucoup plus souvent l'auxiliaire avec laquelle elle a les contacts les plus fréquents femelle β de PARDI) que les autres sujets. Ces luttes aboutissent parfois à la dissolution de la société polygyne. Il suffit de remplacer le nid par un autre (à couvain normal, ou simplement vide) *avant* que l'intolérance de la pondreuse principale n'ait pris un tour trop aigu pour que le calme se rétablisse dans la société. Avec les bonnes reproductrices, notons que ces luttes restent toujours, au plus, bénignes. Le relais nutritiel des ouvrières rétablit un couvain normal, et la société polygyne persiste (2). Dans les sociétés constituées par une femelle accompagnée d'ouvrières, les effets du couvain abortif sont analogues : on observe une grande irritabilité et des bagarres entre sujets.

L'attitude *systématiquement* hostile de certains sujets met vraisemblablement en jeu des réactions du type *réaction à vide*. A cet égard, les effets du couvain abortif sont caractéristiques : il suffit, à ce moment, d'infimes modifications pour provoquer le comportement décrit sous le nom de « massacre du couvain » (cf. 3) ; par exemple : un changement dans la position relative du gâteau (placé verticalement s'il était auparavant dans le plan horizontal), la projection de fumée, l'anesthésie des sujets, des interventions de l'observateur, etc.

2° Certains observateurs (VON SIEBOLD, 1871 ; PARDI, 1951) ont prétendu que les Polistes pillent parfois les nids de sociétés faibles. Nous ne l'avons jamais constaté. Par contre, nous avons remarqué plusieurs fois des manœuvres qu'un observateur non averti prendrait pour un « pillage ». Quand un nid, notamment en fin de saison, contient du couvain abortif, des Guêpes étrangères peuvent participer au « massacre » du couvain. Or, fréquemment, dans ce « massacre », les larves ou les nymphes (à moins d'être trop « abortives ») sont débitées, malaxées et utilisées comme nourri-

(1) Et aussi sur la fécondité.

(2) Nous ne partageons pas les vues de PARDI (lutte pour la position α dans la hiérarchie sociale) sur la signification de cette modification des rapports sociaux.

ture. Il arrive donc que les sujets étrangers rentrent à leur nid avec ces morceaux, comme au retour d'une chasse normale, et les servent à leurs propres larves. On croirait ainsi assister au pillage du nid « faible », par les Guêpes voisines, du nid « puissant ». L'observation attentive dévoile l'erreur de cette interprétation. On constate notamment qu'une fois la pelote de nourriture prête la Guêpe étrangère peut fort bien nourrir (ou essayer) les larves restantes du nid. Indiquons d'ailleurs qu'un nid sain, *sans adultes*, placé à côté d'un nid « fort » provoque la capture d'ouvrières, qui abandonnent souvent leur propre nid (surtout s'il entre dans une phase de couvain abortif). Il peut même arriver que des Guêpes travaillent indifféremment sur deux nids voisins.

3^o Nous n'insisterons pas sur le phénomène bien connu décrit sous le nom de « massacre du couvain ». Selon nous (DELEURANCE, 1952 *a*), ce comportement n'a rien de mystérieux : il représente les réactions caractéristiques des Guêpes en présence d'un couvain] devenu très abortif. On peut le provoquer à tout moment de l'évolution du nid, notamment en passant sur le gâteau un pinceau trempé dans un extrait alcoolique de larves abortives. L'ampleur du phénomène, à l'automne, provient de ce que, les sociétés n'ayant plus de bonnes nourrices, l'avortement du couvain est général. De ce fait, les réactions des Guêpes deviennent très vives.

G. — CONCLUSIONS GÉNÉRALES

Nous avons cherché, dans ce travail, à faire une mise au point du problème éthologique posé par l'existence des phases couvain normal et couvain abortif, en fonction de données nouvelles obtenues depuis 1952. La cause alimentaire du phénomène semble acquise. Il reste cependant à prouver définitivement si cette cause est de nature qualitative ou quantitative. Les recherches de RABATÉ (1954) et les nôtres paraissent favorables à la première ; les glandes labiales sécrèteraient des substances oligodynamiques indispensables au développement normal du couvain. Toutefois, certaines observations semblent indiquer que le facteur quantitatif peut également intervenir. Nos expériences sur la nature des proies chassées montrent l'importance de leurs effets sur la phase couvain abortif. Quelle que soit l'origine du phénomène, l'existence du couvain abortif chez le Poliste s'oppose, notamment par ses séquelles, à la pérennité de la société.

Finalement, nous passons en revue les différents effets observés du couvain abortif sur le comportement reproducteur et social de la Guêpe.

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THE COLLECTION OF FOOD BY BUMBLEBEES

by

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INTRODUCTION

Although there are numerous records of the time factors involved in the collection of food by honeybees, and of the amount collected per trip, relatively little information of this kind is available in the case of bumblebees. The present work was undertaken to obtain this information.

OBSERVATIONS IN THE FIELD.

Each colony was housed in a nest-box which was placed on a shelf behind a large wooden screen. A glass entrance tunnel connected the nest-box with the front of the screen, behind which the observer sat and recorded the incoming and outgoing bees, each of which had been given an individual distinctive marking.

When a reference is made to a 'pollen load' and a 'pollen-gatherer' it is assumed that in many cases the bee concerned was also carrying nectar (BRIAN, 1952; FREE, 1955). The terms 'nectar load' and 'nectar-gatherer' are only used when the forager in question had not been gathering pollen.

All the following observations were made in good weather conditions. Time is recorded as G. M. T.

The foraging population.

On 3 days in August 1951 representative counts were made of the numbers of bumblebees and honeybees which were foraging in a field of red clover. Four areas (each 100 yards \times 2 yards) of the field were chosen, along the long sides of each of which the observer walked every hour, and counted the bees present (fig. 1). The peak of foraging activity for bumblebees and honeybees occurred between 10.00 and 11.00 hours. Only the numbers of honeybees which visited the crop on 21st and 23rd August are shown since on the 25th August none were observed to be present. In comparison with bumblebees, the honeybee population rose to a peak and then fell again more rapidly on each of these two days.

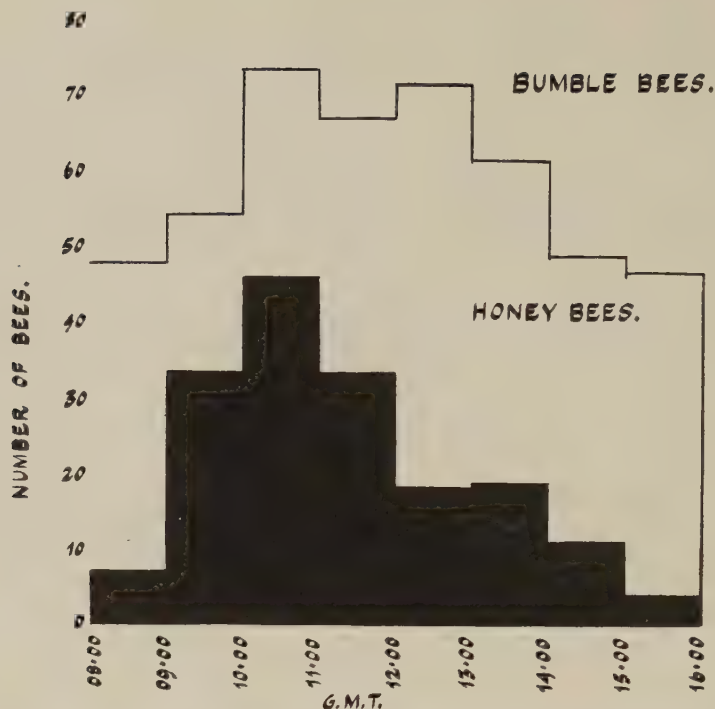


Fig. 1. — Mean number of bumblebees and honeybees counted on 4 strips (100 yds \times 2 yd) of a red clover field on 21, 23 and 25 August, 1951.

Similar peaks of activity were recorded in August 1952 and 1953 although fewer bees were present.

Figures 2 and 3 show the percentage of the bees belonging to a *Bombus*

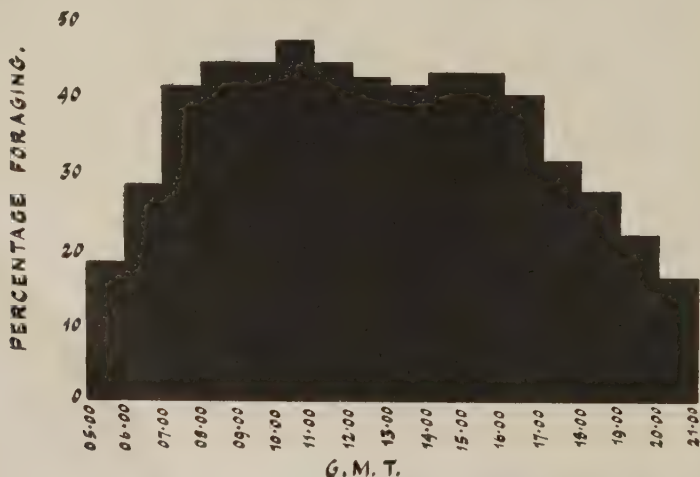


Fig. 2. — Mean percentage of the population of a *Bombus lucorum* colony foraging at different times of the day during 22, 25 and 28 July, 1952.

lucorum and to a *Bombus sylvarum* colony which were foraging during different hours of the day. The colonies were situated at the side of a red clover field and the results agree in general with those obtained by making counts of the foraging bees on the crop and indicate that the proportion of the population which foraged remained fairly constant throughout the greater part of the day.

Several of the foragers spent the night away from their nests. The percentage of foragers of *B. lucorum*, *Bombus pratorum*, and *B. sylvarum* colonies which had not returned to their nests by dark was 22.5 % (mean of 3 days), 13.0 % (mean of 5 days) and 7.5 % (mean of 2 days) respectively.

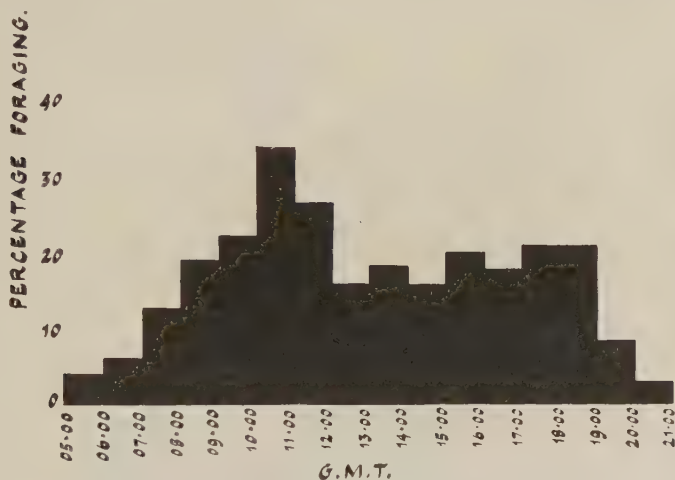


Fig. 3. — Mean percentage of population of a *Bombus sylvarum* colony foraging at different times of the day during 29 and 31 July 1952.

There was no tendency for any particular individuals to stay out; nectar- and pollen-gatherers did so in approximately equal numbers. Such bees had not, apparently, collected full nectar or pollen loads by dusk. The higher percentage of the population of the *B. lucorum* colony which remained away from the nest at night probably resulted from the fact that these foragers took longer to collect nectar and pollen loads than did the foragers of other species.

The collection of nectar and pollen throughout the day.

The number of nectar loads and pollen loads collected at various times of the day by foragers of the *B. lucorum* and *B. sylvarum* colonies are shown in Figs. 4 and 5 respectively. The proportion of pollen loads to nectar loads which were collected by the foragers of both colonies increased during the day. Nectar-gathering reached a peak early in the day and then fell off rapidly. Ten minute counts made each hour in a field of red clover, also showed that the proportion of pollen-gatherers to nectar-gatherers increased during the day. This result was not considered to be associated with

the availability of pollen since the latter was collected about as early in the day as nectar, and the time taken to collect pollen loads steadily increased during the day. It may have been due to nectar becoming scarce, but it is thought probable that large quantities of pollen were only collected after the nectar stores that had been used during the night

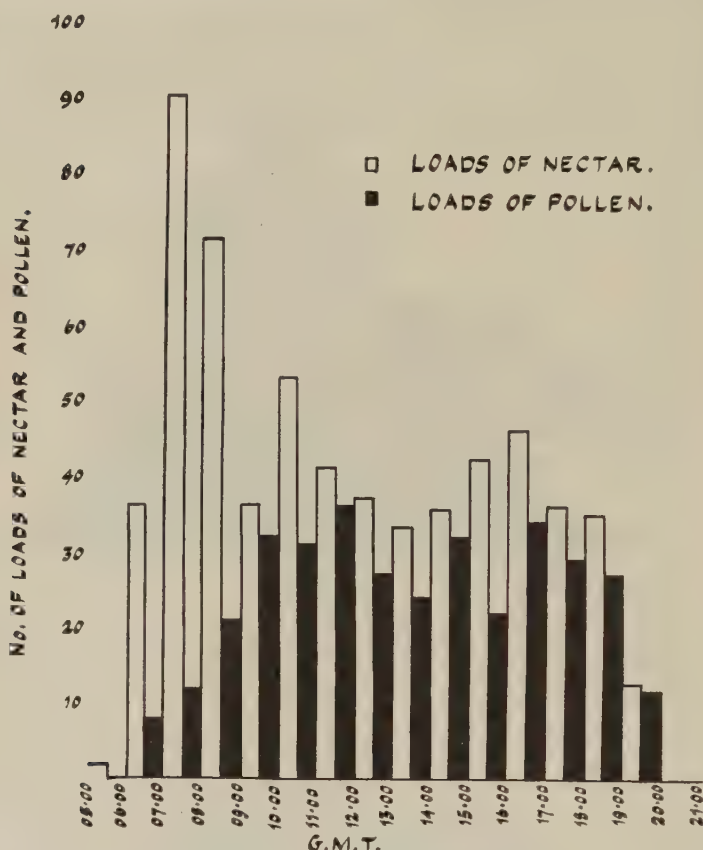


Fig. 4. — The number of loads of nectar and pollen collected at different times of the day on 22, 25 and 28 July 1952 by members of a *B. lucorum* colony.

had first been replenished, as FREE (1955) found that the foragers of a colony only collected pollen when the carbohydrate stores of their colony had reached a certain minimum level.

Time spent on foraging trips.

The data obtained on the time spent by individual members of *Bombus agrorum*, *B. pratorum*, *B. lucorum* and *B. sylvarum* colonies on foraging trips are summarised in Table 1.

The records relating to each colony are taken from the data obtained

only on those days on which both nectar and pollen were collected. The data obtained from the *B. lucorum* and *B. sylvarum* colonies on the same days are quoted for comparison.

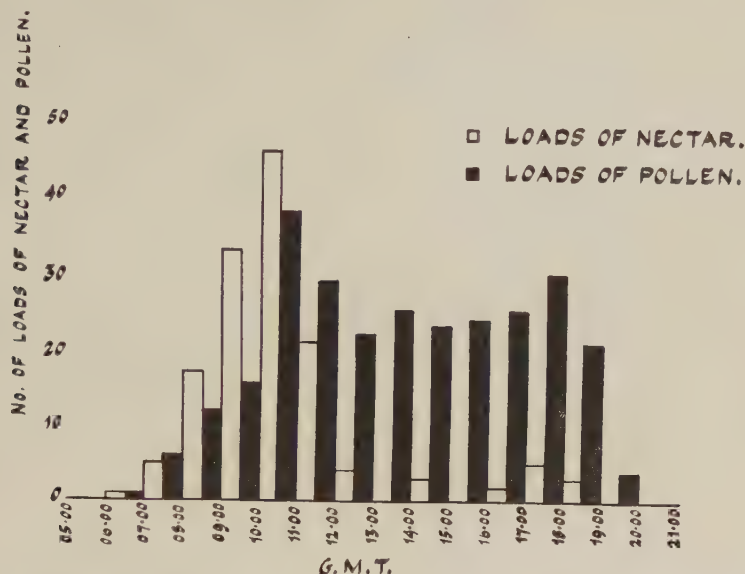


Fig. 5. — The number of loads of nectar and pollen collected at different times of the day on 29 and 31 July 1952 by members of a *B. sylvarum* colony.

The *B. agrorum*, *B. lucorum*, and *B. sylvarum* colonies were situated beside a red clover field. Pollen-gatherers of the *B. agrorum* and *B. syl-*

TABLE 1. — Time spent on foraging trips. (No. of trips given in brackets.)

SPECIES.	DATE of observation.	TIME (MINS.) for collection of loads of nectar.			TIME (MINS.) for the collection of loads of pollen.		
		Mean.	Mode.	Range.	Mean.	Mode.	Range.
<i>B. agrorum</i> .	August 1952.	20.3 (190)	17-19	4-49	22.4 (97)	17-19	7-60
<i>B. pratorum</i> .	May & June 1952.	20.0 (236)	9-11	5-57	33.3 (69)	11-13 17-21	5-85
<i>B. lucorum</i> .	22, 25, 28 July 1952.	53.6 (462)	30-40	7-330	128.9 (187)	120-130	15-360
<i>B. sylvarum</i> .	22, 25, 28 July 1952.	12.7 (23)	—	—	17.5 (47)	—	—
	29, 31 July 1952.	12.4 (130)	9-11	6-45	19.2 (273)	21-23	10-96

varum colonies only collected loads of red clover pollen, but 42.8 % of the pollen loads collected by *B. lucorum* foragers were from other flower species.

Bees took longer to collect loads of pollen than to collect loads of nectar only. The lengths of foraging trips tended to increase slightly during the course of a day. *B. lucorum* foragers tended to take much longer making each trip than foragers of the other species; this was probably due to their larger mean body size.

The above results in respect of the *B. agrorum* colony are similar to those obtained by BRIAN (1952).

Number of foraging trips per day.

Data was collected on the number of trips made per day by *B. lucorum* and *B. sylvarum* foragers. Since relatively few bees collected only nectar or always pollen throughout a day, and since such bees made relatively few trips per day, the data on nectar- and pollen-gatherers have been considered together. *B. sylvarum* foragers made 10.7 trips per day (mean of 2 days) (range 1-27) whilst *B. lucorum* foragers made only 4.3 trips per day (mean of 3 days) (range 1-17).

Duration of time spent in nest.

The lengths of time which foragers spent in their nests between trips were recorded. The data which are given in Table 2 were recorded only on those days on which both nectar and pollen were collected. Any nest-stay of 11 minutes or more is not included as it was assumed that the bees concerned were no longer foraging regularly. (The figures for pollen-gatherers do not include bees which left their nests without having deposited their pollen loads.)

TABLE 2. — *The duration of time (mins.) which foragers spent inside their nests, between foraging trips.*

SPECIES.	NECTAR-GATHERERS.			POLLEN-GATHERERS.		
	No. obser- vations.	Mean.	Mode.	No. obser- vations.	Mean.	Mode.
<i>B. agrorum</i> ...	226	1.7	1-2	91	2.9	2-3
<i>B. pratorum</i> ..	239	1.9	1-2	53	2.7	2-3
<i>B. sylvarum</i> ...	145	2.2	1-2	308	3.4	2-3
<i>B. lucorum</i> ...	468	3.8	3-4	203	5.3	4-5

The mean duration of nest-stays in each species was greater for bees carrying pollen than for those which had collected nectar only. This was probably because the majority of the pollen-gatherers also had nectar to

deposit. The foragers of the colony of *B. lucorum* remained in their nest between trips for longer periods than foragers of the other species.

The relationship between the sizes of individual bees and the weights of their pollen loads.

The pollen loads were removed from 42 *B. terrestris* pollen-gatherers when they returned to their nest. The weights of the pollen loads obtained from the different individuals varied between 2.0-77.0 mg. (mean 24.7 mg.). This variation was too great to be accounted for by the fact the pollen loads were not necessarily obtained from the same plant species. Several of the smaller bees were found to have collected relatively large loads of pollen for their size and vice versa, but the mean weight of the pollen loads of the 22 bees with body weights greater than the mean was 30.4 mg. compared with 18.4 mg. for the pollen loads of the 20 bees whose body weights were less than the mean.

CLEMENTS and LONG (1923) produced data indicating that the mean weight of 61 pollen loads collected by 4 species of bumblebees was 21.6 mg. (range 1.8-73.0).

OBSERVATIONS IN THE LABORATORY.

The uptake of sugar syrup by bumblebees.

The uptake of sugar syrup by worker bumblebees was investigated in order to gain more information about the collection of nectar by foragers under natural conditions.

The workers of a *B. sylvarum* colony were starved for 24 hours and after being weighed individually were allowed to feed on sugar syrup of a predetermined concentration. Wire-gauze was placed over the feeders so that they could only reach the syrup with their tongues. The time which each bee spent feeding was recorded, and each was weighed again immediately afterwards so that the volume of sugar-syrup of each concentration which the individual bees had drunk could be calculated. This procedure was repeated every 24 hours for 7 days. Several bees died during the experiment so that although 39 bees were tested on the first day only 10 were still alive on the seventh day.

[TABLE 3. — *Ingestion of sugar syrup by 10 B. sylvarum workers.*

SUGAR concentration (wt. of sugar to wt. of water).	DATE.	No. obser- vations.	MEAN WT. (mg.) of sugar syrup ingested.	MEAN VOL. (mm. ³) of sugar ingested.	MEAN VOL. (mm. ³) of sugar syrup per ingested sec.
33.3 wt./wt.	7 & 12 Aug.	20	43.6	38.3	52
50.0 wt./wt.	8 & 11 Aug.	20	48.0	39.7	50
66.6 wt./wt.	6, 9, 10 Aug.	30	56.0	43.2	28

The amount of syrup ingested varied greatly in different individuals, and with the same individual at different times. The smallest quantity ingested was 23.1 % and the largest amount was 91.1 % of the unladen body weight of the bees concerned (mean of 52.7 % for 203 loads of syrup). The mean volume of syrup ingested per bee was 44.9 mm.³ and the mean weight of an unladen bee was 107.2 mg.

Since it may be argued that the results obtained in these trials may have been affected by the different physiological conditions of the bees used, only data obtained from the 10 bees which were present throughout the experiment were analysed statistically (Table 3). Analysis of the data showed that there was a highly significant difference ($P < 0.001$) between the weights of the different concentrations of sugar syrup taken up. Although there was a tendency for the volume of syrup taken up to vary with its concentration the results were not significant. There was a highly significant difference ($P < 0.001$) between the rates at which the different concentrations were ingested which is probably explained by the different viscosities of the solutions. The order in which the different concentrations were offered to the experimental bees had no noticeable effect.

In order to investigate the effect of the size of a bee on its uptake of syrup the results obtained each day with bees which were above the mean weight were compared with those obtained with bees below the mean weight. On each of the 7 days both the volume and weight of syrup ingested by the larger bees were greater than those ingested by smaller ones; but the weight increase calculated as a percentage increase in the unladen body weight of each bee was greater in the case of the smaller bees. The division of labour amongst the worker bumblebees of a colony in which the larger bees tend to become foragers and the smaller ones act as house-bees (RICHARDS, 1946) is thus advantageous in that the larger bees collect larger nectar loads.

The rate of uptake of syrup was also greater each day in the case of the larger bees, although the relative rates of drinking of larger and smaller bees were not appreciably affected by the different sugar concentrations. It seems probable therefore that larger foragers collect nectar from flowers more quickly than do smaller foragers, although owing to the larger capacity of the former the time spent on each foraging trip is probably as great.

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Summary.

1. The size of the foraging populations of bumblebee colonies remained fairly constant throughout the day with a peak between 10.00 hrs. and 11.00 hrs. There was a tendency for the proportion of pollen loads to nectar loads collected to increase during the day. About 15 % of the foragers of bumblebee colonies spent the night away from their nests.

2. There was a large variation in the number of trips per day made by bumblebee foragers. Foragers which collected pollen spent longer per trip than those which collected nectar only, and spent longer inside their nests between trips. *B. lucorum* foragers made fewer trips per day and spent more time on each trip than did the other species studied (*B. agrorum*, *B. pratorum* and *B. sylvarum*).

3. The rate at which bumblebees drank sugar syrup depended on the concentration of the syrup and the size of the bee. Larger bumblebees ingested larger volumes than smaller bumblebees, although the latter collected larger loads in proportion to their body size. Individuals varied greatly in the size of pollen loads that they collected.

OBSERVATIONS ON *MACROTERMES GILVUS* HOLMGR. IN JAVA

by

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Ever since the author became acquainted with GRASSÉ & NOIROT's interesting accounts of their investigations on *Macrotermitinæ* of Africa (1944, 1945, 1951) he has felt impelled to work out his own notes on *Macrotermes gilvus* in Java, a great part of which have remained unpublished so far. These observations — and those on several more termite species other than *Neotermes tectonae* Damm. — were not part of the author's official working programma, but were made more or less incidentally whenever opportunity presented itself, mostly during duty tours in the teak forests of Central and West Java. Although rather fragmentary on this account, the notes and photographs collected over a number of years, may yet prove to be of value, especially as they afford material for a comparison with the data published by other workers in South East Asia and with the results of the work of the French termitologists. It is the author's intention to deal successively with several details of the interesting and complex biology of this highly developed termite. As a preliminary to his own observations a short survey will be given of the previously published particulars on the inner structure of *Macrotermes* mounds in Asia.

I. PREVIOUSLY PUBLISHED DETAILS ON THE STRUCTURE OF ASIATIC *MACROTERMES* MOUNDS

The earliest particulars on the inner structure of the mound of an Asiatic *Macrotermes* species can be found in a paper of HAVILAND (1898), who also published a drawing — made after a photograph taken in Sarawak, Borneo — of a vertical section through the centre of a 6 foot high mound of '*Termes malayanus*'. No detailed description of the nest is given, but in the caption of the illustration the author points out: 1) the 'Queen's cell, surrounded by delicate laminae of clay', and: 2) 'Fungus-beds, occupying irregular cavities throughout the periphery of the nest'. The drawing shows a conical mound with steep sides, much broadened at the base. The wall

is about 16-40 cm. thick. The upper half of the inner part is occupied by an accumulation of large combs, the centre of the lower half consists of a subglobular cavity, some 70 cm. high and 80 cm. broad, filled with horizontal clay laminae, which enclose the cell somewhat eccentrically. The layer of comb-containing chambers is extended into the soil beneath the outer part of the gradually sloping base.

The 6 page paper of UICHANCO on 'General facts on the biology of Philippine mound-building termites' (1919) deals exclusively with *M. gilvus*. Some 25 lines are devoted to a description of the inner structure of the mounds. After the thick crust and the fungus gardens beneath it have been mentioned the description reads: 'In a typical anay mound these gardens occupy the greater part of the inner cavity; compact slabs of clay, with numerous irregular passageways running through them, form the partitions and, at the same time, the supports of the gardens' (p. 60). A little further the author continues: 'An upright, irregular shaped pillar of clay which forms the core of the nest serves the double purpose of supporting the series of fungus gardens and of being the main prop that prevents the outer shell of the nest from collapsing.' This feature and the interpretation of it appear to be at variance with observations made elsewhere on the structure of *M.* mounds by others, including the present author. We shall discuss the point later on, but want to mention here that the outer wall owes its solidity to its thickness and its being built as a vault. On page 61 of UICHANCO's paper it is stated that the royal chamber is located a little below the surface of the ground. His plate I gives a photograph of the vertical section of a mound, which is apparently a recently built or expanded one as the vegetation of grasses and climbers does not reach higher than half way up the massive looking clay dome. It clearly shows the layer of combs on the inner side of the wall, enclosing a cavity with smaller, empty holes in the centre (no pillar at all). The basal part below the soil level has not been laid bare.

JOHN (1926) reproduces one clear photograph of a section through a *M. carbonarius* Hag. mound in the jungle of Malaya and two of sections through *M. gilvus* mounds in Malaya and Sumatra. The former shows a cupola-like hill, about one m. high and 2 1/2 m. broad, the surface thickly covered with low vegetation. The exposed inner part shows a limited number of comb-containing chambers embedded in an apparently massive clay mass. The *gilvus* mounds differ a good deal in appearance. The Malayan one, conical in shape, flattopped, some 0,8 m. in height and 2 m. wide at the base, is built against a big prostrated trunk. On one side a large cavity is laid open which contains an accumulation of combs. The outer wall is about 15 cm. thick in that place. For the rest the section runs through a massive clay body. The centre of the mound with the parental cell had not yet been reached apparently. The second mound, rising free from a grass plain, is cylindrical in shape with a rounded top, the wall is about 15-25 cm. thick and surrounds an irregular system of mostly horizontal clay plates enclosing alveoles of very different shapes. Those of

the upper half are the largest and appear to have contained the combs, those in the lower portion are small and flat and in their centre the cell is seen slightly above the base of the section. In the text the following information is given (p. 385): 'Im Bauplan sind die Nester von *M. carbonarius* denen von *M. gilvus* sehr ähnlich.' 'Wie bei *M. gilvus* bildet die Königskammer einen grossen, dickwandigen, festen Klotz mit geglätteten Aussenwänden. Er ruht auf vertikalen Wänden und Säulen und ist von den Seiten und oben durch eingebauten horizontale dünne Wände gestützt. Die Kammern mit den Pilzgärten sind, wie bei allen pilzzüchtende Arten, vorzugsweise an der Peripherie des Nestes angelegt.' For details on the 'Architektur des Nestes und die Struktur der Pilzgärten' the author refers to the photographs, giving no further explanations. He considers the nest reproduced by HAVILAND as relatively young, 'wie die schräg abfallenden, an der Basis sehr dicken Seitenwände bezeugen' (p. 386). This is evidently a mistake as an entirely epigeic nest of the given dimensions must be quite an old one in this species.

BATHELIER, in his remarkable *Contributions à l'étude systématique et biologique des Termites de l'Indochine* (1927, p. 189-196), draws a general picture of the internal structure of *M. gilvus* mounds. He distinguishes: 1) the outer wall, 20-30 cm. thick on an average, at some points pierced by very narrow galleries leading to the exterior; 2) the enclosed part comprising chambers with thin clay walls (région des chambres à parois minces) divided into an outer layer of rooms which contain the fungus combs and are situated right beneath the wall, and a central part occupied by numerous smaller and empty cavities with very thin and fragile walls, in the midst of which the thick-walled lump containing the royal cell is found; 3) the basal part comprising large, properly built cavities (des loges nettement édifiées) gradually passing into simply excavated rooms (seulement creusées) which contain piles of small-cut vegetable matter. These cavities and the connecting large runways extend up to 80 cm. below soil level and 1 m. outward from the circumference of the nest. BATHELIER does not state how many mounds he has inspected, and gives additional details on one mound only, which occupies an abnormal position (on the border of a steep slope and just beside a rock), for the rest referring to a photograph of the vertical section of a greatly extended mound, apparently situated in a plain.

KEMNER carried out his intensive studies on termite life in a few parts of Indonesia in 1920-1921 (the results were published in 1934), but owing to the fact that he worked mainly in the neighbourhood of Bogor (then Buitenzorg) where *Macrotermes* has most of its nests underground, only few large mounds were investigated. He was the first, however, to give details on young nests — which, by the way, are always wholly subterranean — and describes their gradual growth (p. 187, 188). The relatively young nests consist of a thick layer of combs enclosing a core containing the royal cell. The central part is enlarged more and more, and finally forms a mass of 'Galerien' (more properly alveoles), consisting of thin clay

lamellae and pillars. For further enlargement additional cavities are built at some distance from one another, which contain accumulations of combs, while one of them may be used for storing vegetable matter. In still older nests the partitions between the separate cavities — of which up to six have been counted in one nest — are removed and a coherent chain of combs comes into being. The alveolate part with the royal cell may temporarily be in an eccentric position. The next phase appears to be the building of the first epigeic part which may be a hill of 20 cm. in height and 50 cm. wide only. New cavities are excavated and the mound increases in bulk, reaching a height of one m. and more. KEMNER found no passages through the outer wall connecting the nest proper with the exterior except during the swarming season. He described the first part of runways radiating from the nest as nicely constructed and well finished being provided sometimes even with sunken edges like gutters along a street. This author's illustrations include photographs of: *a*) a sideways-opened young mound showing the central cavity and 4 separate comb-filled holes (pl. 5, 1.); *b*) a vertical section of a conical mound, the central part of which containing the royal cell is not exposed (pl. 4, 1.) and: *c*) an opened mound, the inner part of which is obscure and may have been removed already (pl. 8, 1.)

G. A. PANGGA collected data for his 'Biological study on some common Philippine termites' in and around the College of Agriculture campus at Los Baños in 1932-1935. He opened 5 nests of *Macrotermes* out of 25 apparently observed, but gives only a short and superficial description of the inner structure, stating (p. 237) that 'the greater portion of the inner cavity of the mound was occupied by fungus gardens... lodged in niches, a series of which was hewn out in the central clayey pillar of the mound', the different units being connected by numerous passageways. The royal chambers were found after digging 10 to 30 cm. below ground level. A photo-reproduction in his paper (published in 1936) of a vertical section through a conical mound standing in a grass wilderness, is not clear enough to show the necessary details, but it certainly does not show a central pillar. On the contrary, the central basal portion appears to be filled with a narrow-celled structure as found in the *Macrotermes gilvus* mounds elsewhere. Just as in UICHANCO's description it remains doubtful whether the central pillar feature is accurately described. Further elucidation or confirmation is much needed at any rate.

Photographs of vertical sections through *gilvus* mounds examined in the teak forests of Central Java were exhibited by the present author during meetings of entomologists in Bogor in September 1935 and June 1936, and the position of the parental cell above the ground level was especially discussed. Two of the photographs have been reprinted in a paper entitled 'Onze kennis van de Javaanse termieten' (= Our present knowledge of Javanese termites, 1936) and the same pictures may be found as illustrations of the paragraph on *Macrotermes* in the author's book 'De plagen van de cultuurgewassen in Indonesië' (= Pests of Indonesian crops) [p. 172, 175, 1950], where some general remarks about the structure of the mounds

are made. A sketch of the ground-plan of a central cavity of a *gilvus* mound with runways radiating from it was published by the author in 1941*.

This survey of earlier descriptions of the inner structure of *gilvus* mounds brings out how fragmentary and incomplete our knowledge still is and how many details are lacking, while there appear to be some dissimilarities in the features described. As for the central pillar mentioned by the Philippine writers, it may be possible that this refers to a phase in the development of the nest when the mound encloses several comb-filled cavities still separated by clay masses, as described by Kemner. Small galleries perforating the thick outer wall have not been observed by the present author, but they may be present temporarily when the mound is enlarged with new slabs of clay from within. For the release of the winged sexuals in the swarming season crater-like holes are built in the ground at different distances from the mound.

2. FEATURES FOUND IN 'DISMANTLING' GILVUS MOUNDS**

When *gilvus* mounds were first examined by the present author it was found that parts of the strong and thick wall could be broken away without damaging the underlying parts of the nest. In this way groups of fungus gardens could be exposed without damage to the delicate structures. Hence the idea took shape to try to lift off the entire outer wall of the hills piece by piece in order to have a look at the contours of the whole core of the mound, consisting in the nest proper or habitaculum.

The plan was carried out in May 1936, when three mounds were 'dismantled'—as the technique may be called—successively. The operations involved a great deal of work and the efforts were successful only through the efficacious help of a whole team of Javanese personnel and local labourers (fig. 2).

First a rather big mound was tackled (it may indeed be called big in

(*) An actual section through a *gilvus* mound, brought from the teak forests of C. Java was exhibited during the sessions of the 7th. Ned. Ind. Natuurwetensch. Congres held in Batavia (now Djakarta) in 1936. It was a 40 centimetres thick 'slice' obtained by cutting the slopes of a small mound from two opposite sides, including the underground parts. Then the central part was undermined and the supporting ground replaced by a heavy teak board. The remaining vertical section containing and exposing the central cavity with combs, the parent cell, etc., could then be lifted, and was put into a large teak chest and propped with dry grass. It arrived in Batavia in a fair condition, although the solid clay mass and the clay structure in the cavity began to show cracks as the material was drying. Afterwards the chest with its contents—as heavy as a large piano—was transported to Bogor and placed in the museum of the Institute for Research on Plant Pests and Diseases. As the open side was not protected by glass and the drying out process continued, the delicate clay fillings of the cavity supporting the heavy lump of the cell gradually fell to pieces and crumbled away, thereby spoiling the appearance of the exhibit. It is evident that for the preparation of an actual section through a termite-mound for lasting exhibition a device has to be found by which the cracking clay can be held together.

(**) Elaboration of part of the paper read at the 2nd Congress of the U. I. E. I. S. held at Würzburg in April 1955.

comparison with the type of mounds found in the plains and lowlands of Java). The mound had the appearance of a real old hill, somewhat flattened and levelled with gradually sloping sides (fig. 1). The hill was situated under a plot of mixed wild trees, bordering a small glade in the teak plantations. Its subcircular base had a diameter of 3 to 3 1/2 m. The height was about one m. as may be seen in the picture from the size of the Javanese helper standing behind the mound.

Figure 3 shows what the core of the mound looked like after the enveloping crust had been completely removed. The picture is a little confusing owing to the effect of the sunlight filtering through the forest canopy, but it can be seen that the core had an irregular shape. It was more or less like a triangle with its base of 1,2 m. strongly bent inwards, the other two sides 1,8 to 2 m. long. It consisted mainly of a layer of combs built up into small piles in some places and resting on an apparently slightly elevated groundfloor. A few combs lay quite isolated from the rest.

Just beneath the top of the mound a flat and smooth part was bared, which afterwards proved to be the top of the alveolate centre of the habitaculum. It was covered by a thin clay shell, as the close-up photograph of figure 4 shows. This picture further reveals that some of the surrounding, fragile combs had broken down; their shape was somewhat unusual, rather elongated and with large holes.

The parent cell, found in the centre amidst horizontal, thin walled chambers containing masses of young brood, was proportionally small, the nugget measuring only $10 \times 12 \times 5$ cm. It contained a normal 'queen'.

For the second dismantling job, on purpose a much smaller hill was selected, some 60 cm. in height, built against the stump of a felled teak tree. The structure exposed after removal of the crust was rather different from that of the first and showed a more compact body, as may be observed from fig. 5. The picture is more satisfactory than that of the previous core, as a black cloth was used as background, throwing the structure into better relief. The outlines of the core appeared to be nicely rounded and were formed by the upper parts of the closely packed combs, which did nowhere protrude from the body. Some interspaces between them were closed by a smooth clay shell or lamella of the same nature as the one found at the top of the central part in the first mound.

A peculiarity of this nest was that a few chambers did not contain combs but were filled with clay granules apparently formed and piled up by the termites. The colony inhabiting the hill gave an impression of not being very healthy. The nugget of the parent cell measured $17 \times 7 \times 3\frac{1}{2}$ cm.

The third mound opened in the way related above was again a comparatively small one, about 70 cm. in height. When the crust was being removed, a few plant roots had to be ruptured, but no other connection was present between the wall and the core (nor had there been in the two previous mounds). The exposed core presented a very nice picture this time (see fig. 6, which reminds one of an underwater photo of a coral bank on the bottom of the sea !). It again showed a compact body, if this term may be

used for the fragile structure. The combs were not placed so close together as in the previous habitacula and the interspaces were closed again by a smooth clay shell.

The nest appeared to have a second small core or annex, measuring 30 cm. across and situated at some 15 cm. from the body of the main one, which was 65-70 cm. in diameter.

It further appeared after the exposure of the core, that several large alleys radiated from the nest, while one encircled the structure all around. Some runways could be followed for over 1, 2 m. in the surrounding soil. A dense stream of nest inhabitants — part of them workers carrying bits of food — fled from the disturbed nest mainly along one of the thoroughfares.

In the centre of the main part of the habitaculum was the parent cell. A second cell of the same size was detected eccentrically in the same structure and at a lower level. It was occupied only by brood and their worker and soldier attendants.

DISCUSSION

GRASSÉ & NOIROT have found in the nest structure of certain African *Macrotermitinæ* that the habitaculum or 'endoécie' may be partly or entirely separated from the surrounding soil or the enveloping wall by a narrow free space. They have described this in their 1951 publication : *a*) for the comb-containing cavities of *Acanthotermes acanthothorax* ('espace étroit, épais de 3-8 millimètres'), *b*) for the hypogeic part of the nests of *Macrotermes mulleri* ('un espace libre, de faible épaisseur'); *c*) for the whole core of the nest of *M. ivorensis* ('espace libre..... épais d'un centimètre, de telle sorte que l'habitacle se trouve séparé, au-dessus et sur les côtés, de la muraille du nid et, au-dessous, de la terre sous-jacente'), and *d*) in similar fashion as in the last case for the habitaculum of an unidentified *Macrotermes* sp.

In their general considerations, the French authors express their conviction that the free space mentioned is evidently homologous to the 'espace périhabitaculaire' in the mounds of *Bellicositermes natalensis* (*Macrotermes natalensis* in Snyder's catalogus, 1949), described by them in earlier publications and stated to have a width of 3-5 cm. (sometimes less). Furthermore it is suggested by these authors that the feature might be considered homologous also to the free space called 'paraécie' found around the wholly hypogeic nests of *Sphaerotermes* (also a *Macrotermitine* species) and *Apicotermes* (belonging to a different subfamily, as is well known). However, it is realised that these highly specialised nests are very different from the other ones in several respects, and, therefore, it is pointed out by the authors that one needs to be familiar with the early stages of the nest types in question before a definite opinion can be formed about the homology suggested in the latter case. Yet, the French termitologists show themselves prepar-

ed to use their term 'paraécie' in future for every free space around the habitacula ('toutes les cavités périhabitaculaires').

Now the observations made during investigations of the *gilvus* nests, and especially those obtained when dismantling the three mounds, clearly indicate that the epigeic part of the habitaculum in this species has no connection with the protecting wall and therefore is separated from it by a free space. This space is very narrow, apparently only a few mm., and it easily escapes attention when vertical sections of the mounds are made. It must be looked upon, in the author's opinion, as likewise homologous to the 'paraécie' of related *Macrotermitinae* as defined by the French authors in their 1951 paper. Yet, in *gilvus* the paraécie has some peculiar characteristics as it is only present along the sides and upper parts of the habitaculum which are mainly occupied by the comb-containing zone. The basal part of the *gilvus* habitaculum is not separated in the same way from the surrounding soil and this constitutes a real difference especially between the *gilvus* and the *natalensis* mounds in their arrangement. Also the inner construction in the nest of *natalensis* differs markedly from that of the *gilvus* nests in that the habitaculum of the former has several connections with the wall in the shape of thin lamellae and pillars bridging the paraécie.

Another interesting feature which has been brought to light in the exposure of the entire core of the *gilvus* mounds is the clay shell which closes the interspaces between the combs in the surface area of the 'endoécie'. It is particularly well developed in the third dismantled nest, where it constitutes an almost continuous frame provided with large holes where the combs come to the surface.

This thin shell reminds us of the 'lame d'argile' enveloping the endoécie of nests of *M. ivorensis* and called 'idiothèque' by the French authors, but in the latter case it is an almost entire enclosure only perforated by a small number of small or large openings. In the *gilvus* nests the clay shell portions have no perforations and appear to occur only where no combs are embedded in the upper part of the endoécie. Therefore they can be looked upon at best as a partly developed or rudimentary 'idiothèque'.

The term 'idiothèque' was first used by GRASSÉ & NOIROT in their description of the nests of *Acanthotermes acanthothorax*, where the separate parts constituting the endoécie are enveloped by 'une feuille continue en argile... toujours mince, 0,6 à 3 mm... percée çà et là d'orifices ayant de 1,5 à 2,5 mm. de diamètre'. The fungus combs of *Acanthothorax* are therefore wholly enclosed by the shell, and this is again a great difference with what we find in the *gilvus* nests, where the comb-containing cavities communicate with the paraécie.

A well-developed idiothèque is also found in young nests of *B. natalensis*. It is described as: 'Une lame d'argile... percée d'orifices circulaires, peu nombreux, dont le diamètre allait de 0,5 à 2 centimètres... (Elle) n'avait guère plus d'un millimètre d'épaisseur, d'où sa fragilité; elle se soulevait en plis circulaires et superposés qui ressemblaient un peu aux volants d'un jupon de femme. L'enveloppement de l'habitable par une paroi continue...



PLANCHE I.

1. Large *Macrotermes gilvus* hill, before the crust was removed. 2. Team of Javanese persone and labourers who assisted in the 'dismantling' job, standing behind the exposed core of the mound. 3. The exposed core (habitatulum). The small white arrow points to the shell-covered central part. 4. Close up of the shell-covered central part and the surrounding fungus combs.

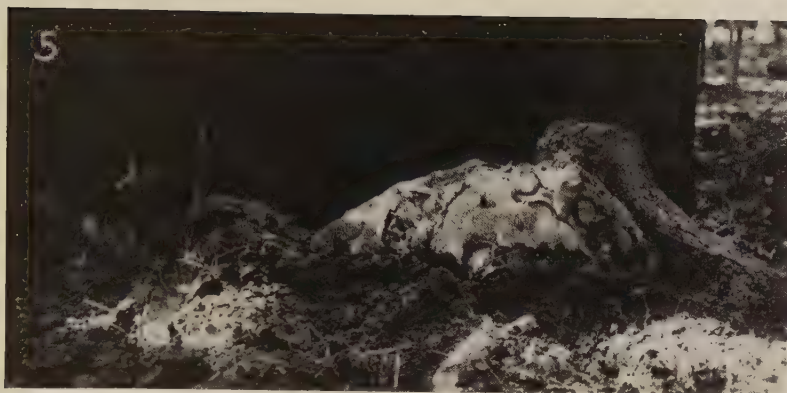


PLANCHE II.

5. Exposed core of the second dismantled hill, built against the stump of a teak tree. 6. Exposed core of the third hill. On the right an annex of the habitaculum. On the left two opened runways radiating from the main part.

est assurément l'un des caractères saillants du nid à ce stade' (GRASSÉ, 1944). In their 1951 paper the French authors point out the striking resemblance between the shell-enclosed endoécie of the *ivorensis* and the young *natalensis* nests. No idiothèque can apparently be distinguished in the upper parts of old *natalensis* nests which have become epigeic.

As for the *gilvus* species, no enveloping shell of the habitaculum portions of still hypogeic, relatively young nests has been mentioned in KEMNER's description (1934), while details on the structure of the very youngest stages of the *gilvus* nests are still entirely lacking.

A further investigation into the possible occurrence of paraécie and idiothèque features in these and other nests must be deemed indispensable for a better understanding of the relationships between various Asiatic and African Macrotermitine species.

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THE REPRODUCTIVE SYSTEM OF YOUNG PRIMARY
REPRODUCTIVES OF *TENUIROSTRITERMES*
TENUIROSTRIS (Desneux)

by

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The reproductive systems of various Isoptera have been the subject of a number of investigations during the past fifty years. These studies have varied greatly in scope and approach, from generalized descriptions of gross morphology to considerations of microanatomical and cytological details. The variations which have been reported by different authors for the same or different genera suggest that further studies are warranted in an effort to obtain a better picture of the apparent variations which occur within the order.

The interest in the termite reproductive system has probably been stimulated to a large extent by the tremendous reproductive potential of a group of insects which have a primitive panoistic ovary. The mature queens of many of the tropical Termitidae become extremely physogastric and deposit many thousands of eggs per day. The only queen of *Tenuirostritermes tenuirostris* which was collected from a well developed colony in the field (WEESNER, 1953) was but slightly physogastric. This individual deposited approximately 300-400 eggs over a twelve hour period. Unfortunately, this queen died in culture and was destroyed by the workers. No information has been obtained regarding the internal anatomy of the fully matured reproductives, which are difficult to find in the subterranean workings of this species. The alates, on the other hand, were readily obtained and are functional at the time of flight.

The young primary reproductives begin depositing eggs within a few days after pairing and as many as 55 eggs may be deposited by a single queen during the first ten days (LIGHT and WEESNER, 1955). This pattern of egg deposition indicates that some of the eggs must be well developed at the time the young primaries leave the parent colony. Furthermore, it seemed probable that there are a larger number of functional ovarioles than are usually attributed to young queens. A superficial examination of the ovaries showed that whereas well developed eggs are present at the time of flight, only a limited number of ovarioles are functional, as will be evident from the subsequent descriptions.

METHODS AND TERMINOLOGY

The specimens which were utilized in this study were preserved in 70 % ethanol during the initial investigation of the mature and incipient colonies in 1946. The present study was not anticipated at that time and little hope was held regarding the histological preservation and staining qualities of the material after such simple fixation and storage until 1954. Actually the material sectioned well in paraffin, was receptive to stains and there was no appreciable distortion.

Forty two individuals were prepared in serial sections at 8 microns. These included brachypterous nymphs, alates and young primary reproductives which had deposited the initial group of eggs. Most of the sections were stained with Alum Hematoxylin and Eosin, a few with Heidenhain's Iron Hematoxylin and others with Mallory's Triple Stain. In addition, carmine-stained whole mounts were prepared of dissections of both male and female reproductive tracts and a number of dissections were made without the preparation of permanent mounts.

Counts of the number of ovarioles were made in four individuals (primary reproductives after the initial egg laying period) by noting the origin of each ovariole, section by section, along the length of the oviduct. In one instance a camera lucida drawing was prepared of each section, so that the fate of each ovariole could be traced. This is the ovary which was utilized in the preparation of figure 4, *b*, *c* and *d*.

In considering the subsequent descriptions, especially as regards the morphology of the ovary, it must be borne in mind that the individuals utilized were functional but had not reached their full reproductive development. The descriptions refer to the structure of the young imagoes unless otherwise specified.

SNODGRASS (1935) has been taken as the standard for terminology. This usage is fairly consistent throughout the termite literature except for the terms sternum, sternite and venter. Sternum refers to a major, ventral, segmental, sclerotized plate. Sternite refers to a subdivision of a sternal plate. Venter refers to the ventral body surface, or the ventral surface of a particular segment.

The term genital chamber, as it is used here, does not follow the strict definition which SNODGRASS (1933) uses in which he distinguishes between a vestibulum and a genital chamber. This distinction depends upon the situation of the pouches above the seventh or eighth venters respectively, with the vestibulum enclosing the genital chamber. Comparable regions will be referred to here as the inner and outer genital chamber. GEYER (1951) uses the term vestibulum and, occasionally, genital chamber, for the same structure. Most other workers have used the term genital chamber or genital cavity (BROWMAN, 1935). Where certain structures are not mentioned by SNODGRASS, an effort has been made to use pre-existing terms on the basis of priority.

In the absence of developmental studies it is not possible to establish with certainty the line of demarkation between ectodermally and mesodermally derived structures, especially as regards the oviduct in the female and the ejaculatory duct in the male. The terminology which is applied to these regions, therefore, is based upon the apparent structures in the adult and should not be considered necessarily indicative of their origin. Likewise, the actual limits between segments seven, eight and nine in the female are indicated by various adult characteristics (musculature, scleritization, etc.) and cannot be considered final without developmental information.

THE FEMALE REPRODUCTIVE SYSTEM

1. — THE GENITAL CHAMBER.

The genital chamber of the female is formed by the overlapping of the eighth and ninth venters by the somewhat elongated seventh sternum (fig. 1). As in other Isoptera, therefore, the seventh sternum forms the sub-genital plate. The floor of the chamber is formed by the enlarged intersegmental membrane between the seventh and eighth venters. The roof of the chamber consists of the venters of the eighth and ninth segments. Both the eighth and ninth venters bear two lateral scleritized and pigmented plates, connected medially and to each other by a membranous sheet of chitin. These sternites bear numerous large and minute bristles on their exposed portions, as does also the seventh sternum. The chitinous membrane lining the chamber lacks bristles. The lateral coria are densely setigerous but bear only large bristles.

The genital chamber includes two regions: an outer, open chamber posteriorly, and an inner, more restricted chamber, anteriorly. The outline of the outer chamber corresponds to the shape of the seventh sternum as it overlaps the ninth venter and the lateral

portions of the eighth. At the medial, anterior portion of the ninth venter is the orifice of the duct from the accessory gland. This orifice is partially enclosed ventrally by the posterior projection of two lips from the eighth venter (fig. 2, *a*). These apparently represent the ventral valves. Anteriorly, between the bases of these two valves, appears the opening of a deep, heavily chitinized groove (fig. 2, *b*) running

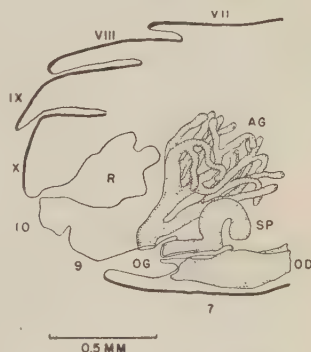


Fig. 1. — Schematic reconstruction from serial sections of the posterior abdomen of a young primary queen. VII-X, tergites; 7, 9, 10, venters; AG, accessory gland; OD, oviduct; OG, outer genital chamber; R, rectum; SP, spermatheca.

along the medial ventral line of the eighth venter. This is the spermathecal furrow ("samerrine" of HOLMGREN, 1909).

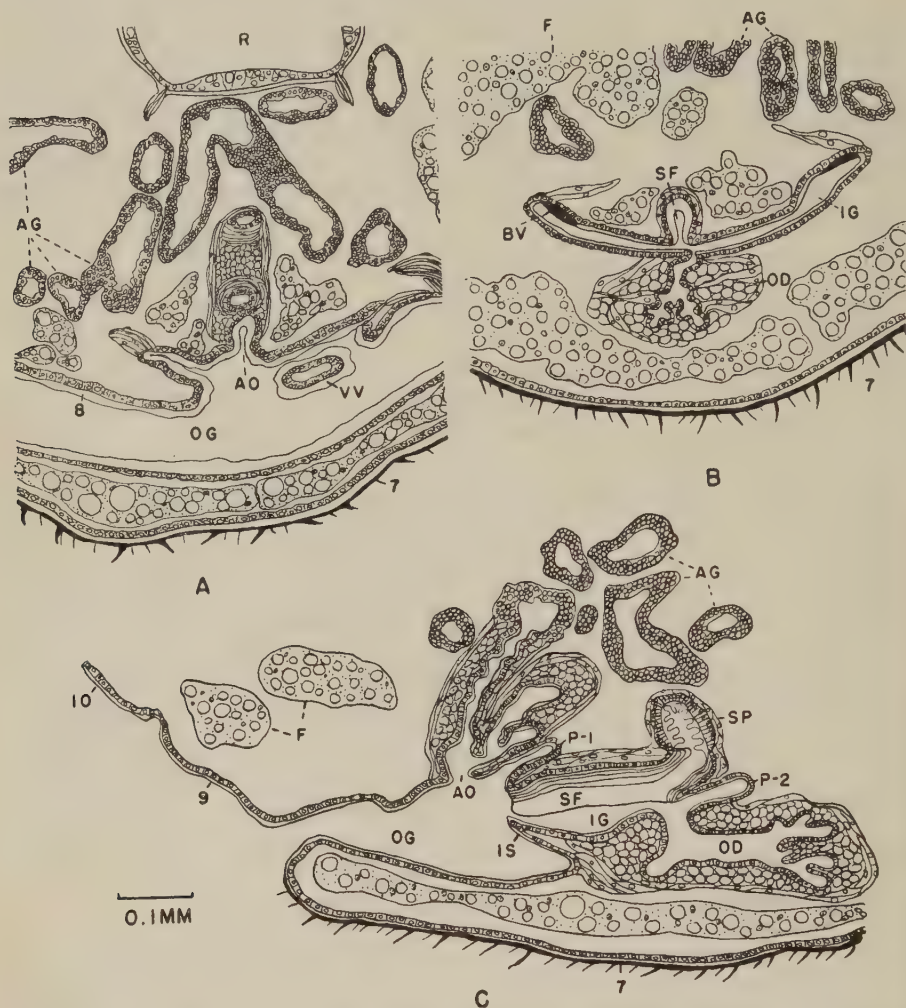


Fig. 2. — Sections through the female genital chamber and associated structures. *a*. Transverse section through medial portion of the outer genital chamber at the level of the accessory gland orifice. *b*. Transverse section through the inner genital chamber at the anterior limit of the spermathecal furrow and the posterior limit of the gonopore. *c*. Sagittal section through the genital chamber. AG, accessory gland; AO, accessory gland orifice; BV, basivalvula; F, fat body; IG, inner genital chamber; IS, intersternal fold; OD, oviduct; OG, outer genital chamber; P-1, pouch between venters 8-9; P-2, pouch at inner end of genital chamber; R, rectum; SF, spermathecal furrow; SP, spermatheca; VV, ventral valves; 7, 8, 9, 10, venters. Camera lucida drawings.

At the point where the spermathecal furrow begins, the genital chamber is restricted ventrally by a fold of the intersegmental membrane between the seventh and eighth venters. BROWMAN (1935) designates this as the

“intersternal fold”. The posterior origin of the spermathecal furrow, above, and the posterior lip of the intersternal fold, below, mark the posterior limits of the inner genital chamber.

The inner genital chamber is compressed laterally as well as dorso-ventrally (fig. 2, *b*). Posteriorly it is about 450 microns wide and tapers slightly anteriorly to about 400 microns. It is approximately 240 to 280 microns long. The spermathecal furrow extends to the midpoint in the chamber as an open groove in the roof. Immediately opposite the anterior limit of the open furrow is the posterior limit of the gonopore which opens through the floor of the chamber (fig. 2, *b* and *c*). The gonopore is slit-like and runs in an anterior-posterior direction. At the upper, lateral margins of the inner genital chamber are two narrow, sclerotized bars (fig. 2, *b*) which apparently represent the basivalvulae.

There are two distinct blind pouches in the genital chamber. The first lies anterior to the orifice of the duct from the accessory glands and above the spermathecal furrow (fig. 2, *c*). The upper wall of this pouch forms the attachment point for two bundles of muscles, right and left, which run to the outer lateral margins of the ninth sternites. This pouch apparently marks the limit between the eighth and ninth venters. The second pouch forms the anterior wall of the inner genital chamber. The ventral, anterior surface of this pouch forms the attachment point for muscles running to the anterior margin of the seventh sternum. Thus, as was indicated earlier, the floor of the inner genital chamber appears to be formed by the intersegmental membrane between the seventh and eighth venters.

2. — THE ACCESSORY STRUCTURES.

The duct leading to the accessory gland divides, usually into anteriorly and posteriorly directed trunks, from which arise the tubules of the gland (fig. 1). These tubules are more or less convoluted and are usually bifurcated. The duct itself is provided with a muscular wall which is absent from the tubules. These tubules are composed of minute and densely crowded cells surrounding a central lumen and enclosed by an epithelial sheath. The function of these glands in the Isoptera has not yet been determined.

The spermathecal furrow consists of a heavily chitinized groove, roughly horseshoe shaped in tranverse section, with the narrow opening along the ventral line. The thickened inner wall is concentrically laminated and is continuous with the thin chitinous intima of the inner genital chamber (fig. 2, *b*). The furrow is enclosed dorsally and laterally by an epithelial layer, resting on a basement membrane, which, in turn, is enclosed by a muscular wall. Although this furrow is present in the pre-imaginal nymphs, the thickened chitinous lining does not appear except in the imago.

At its posterior end the furrow opens directly into the outer genital

chamber. At its anterior end it is continuous with a closed duct (fig. 3, *b, c*) lined with a smooth, concentrically laminated chitinous wall overlying an

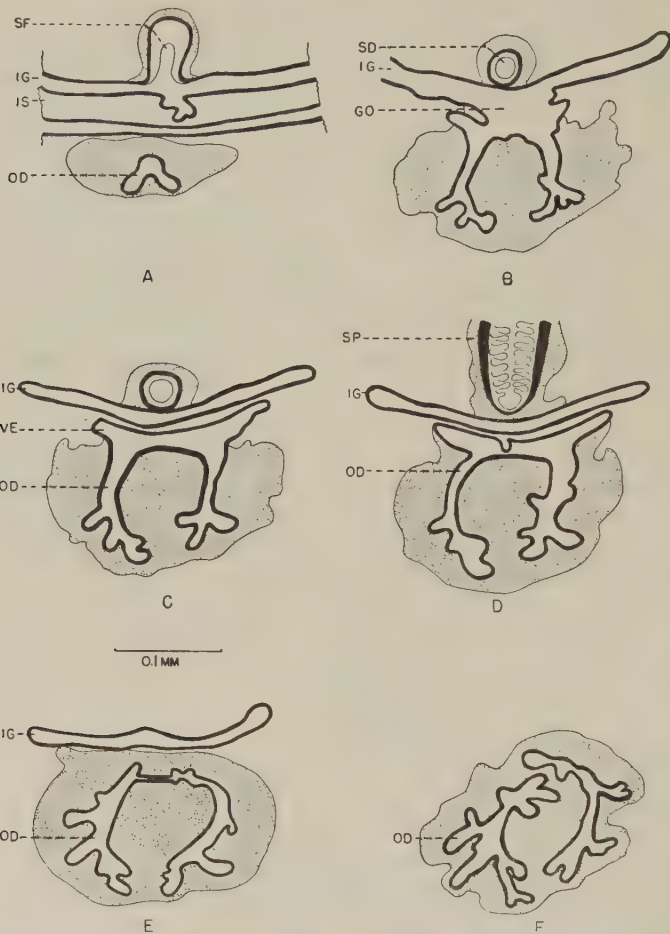


Fig. 3. — Transverse sections through successive areas (posterior to anterior) of the inner genital chamber, gonopore and medial oviduct. *a.* Section through the posterior portion of the inner genital chamber (IG) showing the spermathecal furrow (SF), grooved interstitial fold (IS) and the posterior projection of the medial oviduct (OD). *b.* Section at the level of the gonopore (GO), showing the spermathecal duct (SD) above the inner genital chamber (IG). *c.* Section anterior to the gonopore, showing the thin walled vestibule (VE) below the inner genital chamber. *d.* Section at the level of the spermatheca (SP) showing the dorsal-medial fold in the wall of the vestibule. *e.* Section posterior to the vestibule, the oviducts still interconnected at the dorsal mid-line. *f.* Section of the medial oviduct, internally divided into right and left oviducts. Solid black indicates epithelium; stippled areas denote muscular mass. Diagrammatic, drawn with the aid of a camera lucida.

epithelial layer and enclosed dorsally and laterally by a muscular coat. This duct is attached throughout its length to the upper, inner surface of the inner genital chamber. The spermathecal duct leads into the sper-

matheca which usually arises at a right angle to the duct (fig. 1 ; 2, *c* ; 3, *d*) and runs dorsally.

The general form of the spermatheca is that of a thick blind tube with a recurved end. The inner wall is composed of finger-like projections of chitin beneath which lies a dense eosinophilic layer underlaid by a zone of nuclei. Beneath these lies a rank of tall colymnar cells which are vacuolated and evidently secretory in function. These rest upon a basement membrane which is invested by a muscular tunic. The chitinous lining of the spermatheca is penetrated at 4 to 5 micron intervals by the opening of the intracellular canals ("Ausführgang" of AHRENS, 1935). These canals lead from the lumen of the spermatheca, through the eosinophilic layer and into the columnar epithelium. The canals appear to be invaginations of the chitinous intima and are 1 to 1.5 micron in diameter. They may be as much as 20 microns long, running at various angles from the surface into the epithelium. Both the finger-like chitinous projections and the intracellular canals are lacking in the pre-imaginal nymphs.

All of the females which had been combined with males in culture had sperm present in the spermathecal duct and the spermatheca. In a few instances sperm were also present in the spermathecal furrow.

3. — THE OVIDUCTS.

Superficially, the lateral oviducts appear to join to form a medial duct opening via the gonopore through the floor of the inner genital chamber (fig. 1). A consideration of serial sections, however, reveals a more complex situation. A section through the most posterior portion of the gonopore (fig. 2, *b*) shows a duct having the form of an inverted Y. The stem of the Y represents the gonopore and the two arms represent the extensions of the right and left oviducts. Posteriorly the gonopore is continuous with a medial groove in the intersternal fold. This groove lies opposite the spermathecal furrow (fig. 3, *a*), and probably permits expansion of the chamber when the egg is extruded from the gonopore. Below the intersternal fold, lies a posterior projection of the oviducts which are joined at the apex to form an inverted V in transverse section. They are surrounded by a muscular and connective tissue mass.

Anterior to the posterior edge of the gonopore, the aperture is widened (fig. 3, *b*) and leads into a thin-walled vestibule into the floor of which open the right and left oviducts which are separated and enclosed by a muscular mass. Anterior to the gonopore, the upper, thin-walled vestibule persists (fig. 3, *c*) lying immediately below the inner genital chamber. More anteriorly, at the level of the origin of the spermatheca (fig. 3, *d*) a fold appears in the medial, dorsal wall of the vestibule and the lower arms of the chamber are enclosed by extensions of the muscular wall surrounding the oviducts. At the level where the inner genital chamber ends, the vestibule has disappeared, the right and left portions being continuous

with the right and left oviducts and the whole being surrounded by a muscular mass. Although the right and left oviducts are distinct, they are still interconnected at the dorsal medial line (fig. 3, *e*). Finally, the right and the left oviducts are completely separated from one another internally (fig. 3, *f*), although surrounded by a common muscular mass.

The two ducts separate completely to form the right and left oviducts which extend laterally and then dorsally, in a nearly vertical plane on either side of the gut. The vertical arms of the oviducts lie within the limits of the seventh segment.

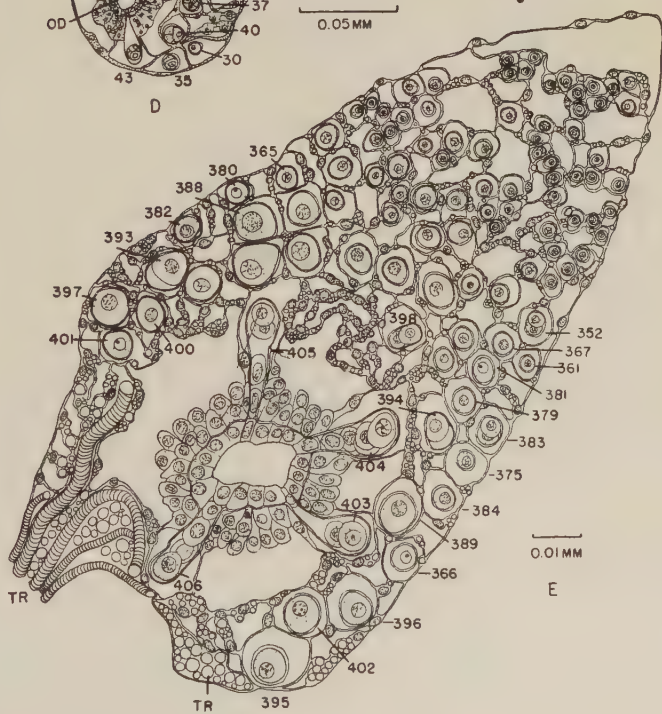
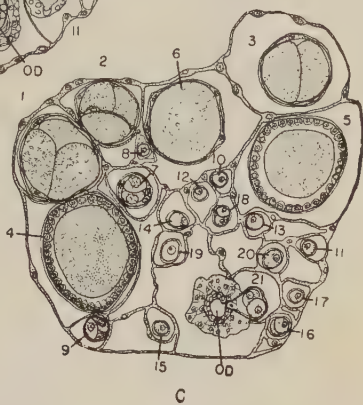
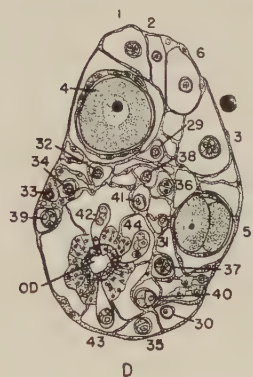
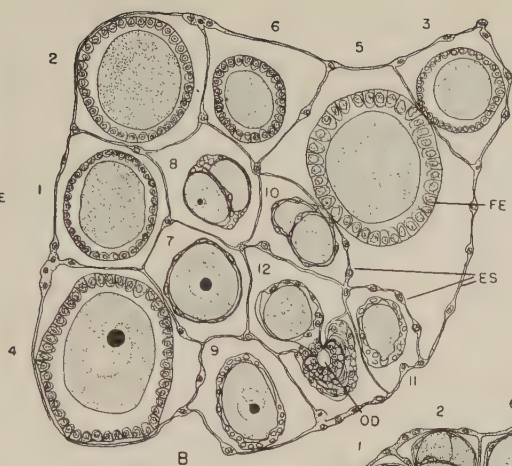
Immediately above the level of the gut, the first ovarioles are inserted into the oviducts. The oviducts extend anteriorly, maintaining a fairly constant level dorsal to and on either side of the gut. At their anterior ends they are slightly more dorsal and medial than at their posterior ends. The oviducts persist for almost the full length of the abdomen, terminating at the level of the first or second abdominal segments. Anteriorly the oviducts lack a muscular wall, the lumen of the duct being surrounded by an epithelial layer and this is enclosed by a mass of connective tissue. A distinct basement membrane underlies the epithelium.

4. — THE OVARY.

Each ovary (fig. 4, *a*) is composed of a large number of ovarioles, arising along the entire length of the oviduct anterior to the vertical arms. The ovarioles arise from all sides of the oviduct (fig. 4) and extend anteriorly and towards the dorsal mid-line of the body from their point of insertion on the oviduct. The total number of ovarioles, as counted in serial sections of one ovary in each of four individuals, was found to be 408, 413, 415 and 450, respectively. Of this large potential, between 800 and 900 per individual, only 5 to 8 are functional in each ovary at the time of flight. The most mature ovarioles are those inserted at the posterior portion of the oviduct.

Each ovariole is surrounded along its entire length by a closely applied, non-cellular layer, the *tunica propria*. Anteriorly, the *tunica propria* encloses three or four elongated epithelial cells, forming the terminal filament (fig. 5). The terminal filament is attached to adjacent cells of the epithelial sheath and the tracheal mass with which the ovary is richly

Fig. 4. — The ovary of a young primary after the initial egg laying period. *a*. Ovary as observed in a whole mount. *b-b* and *e-e* indicate approximate levels of sections *b* and *e*, respectively. *b*. Transverse section through ovary at level where the twelfth ovariole arises from the oviduct. *c*. Transverse section through the last section in which the twelfth ovariole is visible. *d*. Transverse section through the last section in which the first ovariole is visible. *e*. Transverse section through the anterior portion of the ovary. Numbers refer to successive ovarioles as they arise from the oviduct from posterior to anterior. ES, epithelial sheath; FE, follicular epithelium; OD, oviduct; TR, trachea. Trachea have not been shown in figures *a*, *b*, *c* and *d*. Camera lucida drawings.



provided. The terminal filament may be extended into a thin prolonged strand, or may be pleated and recurved as shown in figure 5. Posteriorly, the *tunica propria*

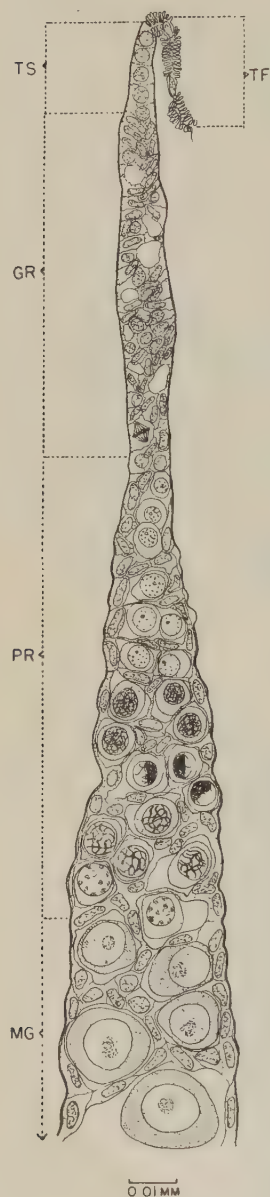


Fig. 5. — Terminal portion of a single ovariole. GR, germarium; MG, middle growth region; PR, prophase region; TF, terminal filament; TS, terminal strand. Camera lucida drawing.

appears to be continuous with the basement membrane of the epithelium lining the oviduct. This relationship is best demonstrated in sections prepared with Mallory's Triple Stain.

In the case of young primary reproductives which have deposited the initial group of eggs, the stalk or peduncle of each functional ovariole is enclosed by a greatly folded sheet of *tunica propria*. A similar structure has been described by AHRENS (1935) in *Odontotermes redemanni*. Apparently the *tunica propria* persists as a continuous layer, although the cells of the follicular epithelium disintegrate after the deposition of the fully developed eggs. The presence of this folded *tunica propria* is helpful in recognizing ovarioles which have released eggs.

Beyond the *tunica propria*, each ovariole is enclosed by loose epithelial sheath of flattened cells (fig. 4, b, c, d and e). These cells are continuous basally with the epithelium surrounding the oviduct. In crowded regions of the ovary the epithelial sheath may be in contact with the *tunica propria* but they do not have any mutual structural continuity. The epithelial sheaths appear to extend anteriorly to form the ovarian ligaments which usually remain separated on the right and left sides until immediately before their attachment in the dorsal portion of the meta-thorax.

The mature ovariole tapers anteriorly and has a typical panoistic organization, lacking specialized nurse cells and provided posteriorly with a well developed follicular epithelium. In addition to the terminal filament, mentioned above, the mature ovariole usually includes five structural areas which are fairly sharply defined from one another. As will be indicated later, the proportion of each region varies from ovariole to ovariole. These areas include: the terminal strand; germarium; prophase or initial growth region; middle growth region; and the terminal growth region. The areas may be defined as follows:

a. *The terminal strand.* Immediately posterior

to the terminal filament lies a strand of small cells with round nuclei (fig. 5). These cells are arranged in a linear series and measure about 4 microns in transverse section. They fill the entire ovariole at this level and are enclosed by the *tunica propria*. Their number varies from as few as four in well developed ovarioles to sixteen in the immature ovarioles. In a few instances, this area could not be distinguished in the most posterior ovarioles, the terminal filament arising directly from the germarium. The origin, function and fate of these cells has not been determined.

b. *The germarium*. Posterior to the terminal strand is an area in which the cells and their nuclei are flattened and closely crowded (fig. 5). In immature ovarioles, these cells may be arranged in a linear series, the nuclei being oriented with their long axes across the ovariole. In mature ovarioles, the diameter of the ovariole may increase suddenly from 4 microns (of the terminal strand) to 8 or 10 microns and the cells are arranged at random within the *tunica propria*. Dividing cells are frequently observed within the germarium, especially in the posterior third.

c. *The prophase region*. The posterior limit of the germarium is marked by the appearance of small round oöcytes surrounded by smaller, elongated epithelial cells (fig. 5). These oöcytes, which are 5 to 6 microns in diameter, mark the anterior limits of the prophase or initial growth region. The oöcytes increase gradually in size until they are 10-14 microns in diameter. The epithelial cells increase slightly in number, but maintain their relatively small size and squamous form. The most distinctive character of this region, as implied by the name, is a conspicuous rearrangement of the chromatin material within the nuclei of the young oöcytes. The most anterior oöcytes have a reticulated chromatin network with a small nucleolus. The latter disappears and the chromatin material is arranged in fine, elongated threads, at first diffuse and then concentrated to one side of the nucleus. Subsequent nuclei contain shorter, thicker chromatin threads, distributed throughout the nucleus. Finally, the nucleoli reappear and the nuclei contain about twenty peripheral clumps of basophilic material which appear to represent clumped chromatin threads. This series of transformations corresponds closely to the typical pregrowth meiotic prophase. Throughout the prophase region, the cytoplasm of the oöcytes is eosinophilic and the chromatin strongly basophilic. The nuclei in the posterior oöcytes reach a diameter of 7.5 to 9 microns and the nucleoli a diameter of 2 to 2.5 microns. The overall cross-sectional diameter of the ovariole increases from about 21 microns anteriorly to about 34 microns posteriorly.

d. *The middle growth region*. Posterior to the prophase region, the oöcytes increase rapidly in size and the cytoplasm becomes basophilic. The developing oöcytes are crowded within the ovariole, either side by side, or in a staggered series, especially towards the posterior end. They are usually ovoid or tetrahedral in shape. The large round germinal vesicle contains a conspicuous nucleolus and peripheral clumps of chromatin material which become diffuse and oxyphilic. Posteriorly, the

nuclei reach a diameter of 14 microns and the nucleoli have a diameter of 5 microns. Each oöcyte is enclosed in a thin sheet of follicular epithelium whose nuclei tend to be grouped in clumps between adjacent oöcytes.

TABLE 1.

Dimensions of Oöcytes in the Terminal Growth Region of Five Ovarioles in a Young Queen.*

OOCYTE **.	FIRST ovariole.	SECOND ovariole.	THIRD ovariole.	SEVENTH ovariole.	NINTH ovariole.
1	210 × 107	252 × 175	210 × 122	120 × 45	48 × 40
2	88 × 59	140 × 70	122 × 70	55 × 70	30 × 36
3	77 × 52	112 × 59	105 × 63	42 × 32	30 × 36
4	77 × 49	112 × 59	73 × 56	25 × 32	27 × 36
5	63 × 45	80 × 58	59 × 49	18 × 32	
6	49 × 45	63 × 52	49 × 49	15 × 32	
7	38 × 45	52 × 49	28 × 42	15 × 32	
8	31 × 42	38 × 42	28 × 42		
9	22 × 42	31 × 42			
10	21 × 38	31 × 35			
11	28 × 38				
12	24 × 31				

* Dimensions given in microns. First figure in each pair is greatest dimensions of oöcyte on the long axis of the ovariole. Second figure is greatest transverse dimension.

** Oöcytes and ovarioles numbered from most posterior to most anterior.

e. *The terminal growth region.* The final growth phase includes a number of oöcytes arranged in a linear series and enclosed in a well defined wall of follicular epithelium. The most anterior oöcytes may be round,

or are frequently flattened across the ovarioles, so that they are wider than long. The oöcytes gradually become elongated in the plane of the long axis of the ovariole.

The general size and shape of successive oöcytes in the terminal growth region is indicated by the examples in table 1. These measurements were taken from sections of a young primary reproductive which had deposited the initial group of eggs. The first six ovarioles on either side of this individual each contained one fairly well developed, yolky egg. Judging by the presence of a pleated *tunica propria* at the base of the peduncles, there were seven functional ovarioles in this ovary. The ninth ovariole, therefore, although containing a few oöcytes in the terminal growth region, was still immature.

The germinal vesicle increases gradually in size and maintains a central position in the oöcyte until the latter have reached a length in excess of 200 microns. The largest central nuclei have a diameter of 24 microns. In oöcytes exceeding 200 microns it was usually impossible to distinguish the nucleus. In a few instances an irregular nucleus, usually with two large, irregular nucleoli could be observe at the periphery of the larger, yolky oöcytes. No maturation spindles were observed, although an effort was made to find them.

The largest contained oöcyte in any of the primary reproductives which were sectioned was 754 by 232 microns. This oöcyte possessed a well developed chorion. The three succeeding oöcytes in this same ovariole were 464 by 233, 406 by 202, and 348 by 174 microns, respectively. This was the first (most posterior) ovariole in an alate taken from the colony workings on the day when alates first appeared in the field colonies, more than a month before the first flight occurred.

As has been indicated earlier, the presence and proportion of the various regions varies from the mature to the immature ovarioles. The bulk of the anterior ovarioles consist only of an elongated germarium, terminal strand and the terminal filament. More posteriorly, subsequent ovarioles include a definite prophase region. Posterior to these the ovarioles also include a middle growth region, and, finally, the last 10 or 11 in young primaries, include a terminal growth region. Only 5 to 8 of these latter are actually functional at the time of flight. Frequently, the most posterior ovarioles lack the middle growth region. In these, the terminal region immediately adjoins the prophase region. This condition, as well as the presence of rather distinct areas of development in all of the ovarioles, suggests a rhythmic rather than a continuous production of oöcytes.

5. — THE FOLLICULAR EPITHELIUM.

The development of the follicular epithelium is comparable to that described by AHRENS (1935) in *Odontotermes redemanni*. I was unable, however, to distinguish with certainty between follicular and germinal

cells in the germarium. The first recognizable follicular cells lie in the anterior portion of the prophase region. These cells are squamous and contain an elongated nucleus with a reticulated chromatin network. Throughout the prophase and middle growth regions, the follicular epithelium is composed of flattened and irregular cells, separating the oöcytes from one another and from the *tunica propria*. Dividing follicular nuclei are frequently observed through these areas.

At the anterior portion of the terminal growth region, the epithelial cells separating the oöcytes from the *tunica propria* become more numerous and assume a flattened cuboidal and, later, a cuboidal form. The cells which separate adjacent oöcytes are squamous in form. By the time the oöcyte reaches a dimension of about 170 by 80 microns, and before active

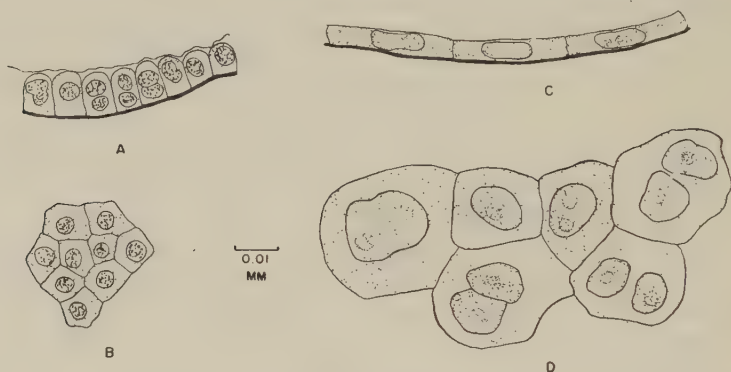


Fig. 6. — Follicular epithelial cells. *a*, section and *b*, surface view of follicular epithelium from an oöcyte of 170 \times 80 microns. *c*, section and *d*, surface view of follicular epithelium from an oöcyte having a chorion. Black line in sectional views represents the *tunica propria*. Camera lucida drawings.

yolk formation occurs, the follicular epithelium is columnar, with a rounded inner surface (fig. 6, *a* and *b*). At this time the cells are frequently binucleate, the nuclei being arranged one above the other. By the time the chorion is deposited, the cells of the follicular epithelium are enlarged and once again flattened, being compressed between the egg and the *tunica propria*. They may be bi- or uni-nucleate, the former cells being appreciably larger than the latter (fig. 6, *c* and *d*).

Subsequent to the deposition of the egg, the follicular epithelium disintegrates and is apparently resorbed. As has been indicated earlier, the *tunica propria* persists as a tremendously pleated sheet, connecting the oviduct with the next follicle. No yellow pigment granules are observed in the area of disintegrating follicular cells, as have been described for various species (BUGNION and POPOFF, 1912; AHRENS, 1935).

THE MALE REPRODUCTIVE SYSTEM

The seventh sternum of the male reproductive is not elongated as it is in the female. It has the same general form and size as the preceeding sterna, being about 2.4 mm. wide by 0.64 mm. deep. Unlike the divided plates in the female, the eighth and ninth sterna of the male are entire, although they are smaller than the seventh. The eighth sternum is about 1.89 mm. by 0.45 mm., and the ninth, 1.31 by 0.22 mm. The seventh, eighth and ninth sterna are all sclerotized, pigmented and densely setose. As in the female, the setae include both a large and minute series on the sterna, whereas the lateral coria bear only large setae. No styli are apparent on the ninth sternum.

The external gonopore lies medially in the intersegmental membrane between the ninth and tenth sterna. In sectioned material this opening can be observed to lie within an invaginated membranous sheath which probably represents a small, distendable penis. The gonopore is continuous with a short, muscular ejaculatory duct which terminates in a round bulbous portion (fig. 7) into which open the right and left vasa deferentia.

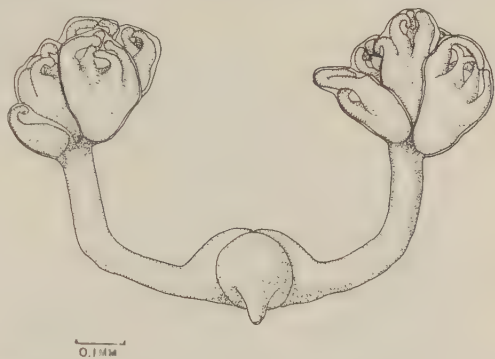


Fig. 7. — The male reproductive system, from a whole mount.

The vasa deferentia open into the ejaculatory bulb via two small openings situated anterior-laterally and slightly dorsal of the midline on either side of the bulb. The basal portion of each vas deferens is slightly enlarged to form a chamber, roughly triangular in form, which evidently serves as a point of sperm storage. Beyond the enlarged basal portion, each vas deferens runs laterally and then dorsally in an almost vertical plane on either side of the rectum to join the testicular lobes.

The testes are minute and lie laterally on either side of the rectum. Each testis (fig. 7) consists of 6 to 8 compound testicular lobes. Each lobe may include 1 to 6 spermatie tubes which are united at the base and open into a chamber, which might be considered the vas efferens, and which empties into the vas deferens. Each sperm tube has a free end distally which is usually recurved and is occasionally bifurcated.

Figure 8 presents a camera lucida drawing of a section transecting two testicular lobes. The terminal portion of each tube consists of a germarium and contains small, closely packed cells among which division figures may occasionally be observed. Histologically the germarium of the testis resembles the germarium of the ovary. Below the germarium, the cells

are enlarged and regular in shape and are arranged in groups or cysts. The nuclei show a reticulated chromatin network. Below this lies an area in which the cells are undergoing prophase phenomena and meiotic divisions. All of the cells within a given cyst divide synchronously. Finally, immediately adjacent to the vas efferens, lie cysts containing spermatids and spermatazoa.

In the upper portion of the vas deferens the sperm are frequently clumped



Fig. 8. — Section through two testicular lobes, showing two spermatid tubes on the left; the terminal portion of one and the basal portions of three spermatid tubes on the right. ES, epithelial sheath; SP, sperm; TR, trachea; VD, vas deferens. Semi-diagrammatic, drawn with the aid of a camera lucida.

into groups, although not enclosed within a cyst. The spermatazoa in the upper portion may be surrounded by an eosinophilic cytoplasmic mass, which is absent from the sperm in the lower portion of the vas deferens. The sperm, as observed in the testis and vas deferens of the male and the spermatheca of the female, are apparently non-flagellated.

The sperm are minute round bodies, staining intensely with hematoxylin or acid fuchsin. Under high magnification they give the appearance of small ring-like structures with a dark periphery and a more lightly staining

central portion. They are about 1.5 to 1.75 micron in diameter. There are also present, in smaller numbers, sperm which are 2.5 to 3.5 microns in diameter, which frequently retain their cytoplasmic envelope. In these cells the basophilic portion is usually irregular and vesiculated. Such "sperm" are probably abortive and apparently disintegrate, since they are not usually encountered in the spermatheca of the female.

GEYER (1951) describes micro- and macrosperm in *Macrotermes natalensis*, but in this species the larger sperm apparently represent the normal elements and are present in large numbers. The larger cells observed in *T. tenuirostris* may be comparable to the sperm nutritive cells which JUCCI (1924) describes in *Kalotermes flavicollis* and *Reticulitermes lucifugus*. STELLA (1938) also observed these cells in the same two species. Both Jussi and Stella conclude that these cells may represent abortive germinal elements which serve a nutritive function for sustaining the matured sperm in the vas deferens and the seminal vesicle.

DISCUSSION

Perhaps the most difficult discrepancy to resolve in the existing literature on the termite reproductive system is the occurrence of a spermathecal furrow. The only description of such a structure, to my knowledge, is that by HOLMGREN (1909) in *Heterotermes* (= *Leucotermes*) *tenuis*. There is reason to believe, however, that such a structure is present in some of the other genera which have been described but that various authors have not made a distinction between a simple pore or spermora and an elongated furrow. AHRENS (1935, b) states that the spermatheca and the accessory gland of *Odontotermes* species and *O.* (= *Termes*) *rede-manni* open posterior to the oviduct. His figures, however, indicate that the opening of the spermatheca lies at the same level as the opening of the oviduct and is extended posteriorly as a furrow. The presence of a furrow is also suggested in BROWMAN's (1935) figure of *Pseudacanthotermes militaris* and it is almost certainly present in *Macrotermes natalensis*, *M. swaziae* and *Odontotermes* (= *Termes*) *angustatus* as illustrated by GEYER (1951). On the other hand, the figures which both of these authors present for species from the lower families of termites do not suggest any prolongation of the spermathecal aperture. Indeed, the sagittal section of *Neotermes zuluensis* shown by GEYER, clearly indicates that the opening of the spermathecal duct is a simple pore in this species.

The spermathecal furrow appears to represent an elongation of the spermora which it resembles histologically. GEYER's transverse sections of the "proximal portions" of the "spermora" of *M. natalensis* and *N. zuluensis* show a striking similarity to one another and to a similar section of the spermathecal furrow of *T. tenuirostris*. However, no scleritization occurs between the thickened chitinous intima and the epithelial layer of the furrow in *T. tenuirostris*, as it does in the "spermora" of the other two

species. I have examined sections of *Reticulitermes hesperus* (BANKS) and in this species the spermora also shows the same general histological organization and has a sclerotized arch. The size of the aperture in *R. hesperus*, however, does not exceed 40 microns as compared with the elongated (120-140 microns) structure in *T. tenuirostris*. HOLMGREN (1909) does not state the length of the furrow in *Heterotermes tenuis*, nor does GEYER (1951) indicate the actual size of the "spermora" in any of the species which he considered.

Functionally, the long spermathecal furrow, opening directly into the outer genital chamber, would seem advantageous in transmitting sperm into the spermatheca. At the same time, the actual opening of the spermathecal duct is maintained opposite the gonopore. The presence of such a furrow is apparently correlated with a long inner genital chamber. In *R. hesperus*, for example, the inner genital chamber is relatively shallow and the spermora relatively small. HOLMGREN (1909) illustrates the oviducts of *H. tenuis* as opening posterior to the termination of the spermathecal furrow. HEBERDEY (1931), in considering HOLMGREN's description, suggests that the spermathecal furrow aids in the transfer of sperm from the anteriorly situated spermatheca to the posteriorly situated gonopore. This, of course, is a perfectly good functional relationship, provided that HOLMGREN's description is correct. Regarding the position and opening of the oviduct, HOLMGREN remarks: „Ich bemerke, daß bei *Leucotermes tenuis* ist dies Verhältnis an meinen Präparaten nicht besonders deutlich sehen. Da aber bei anderen Termitenpräparaten das Verhältnis sehr deutlich hervortritt, so wage ich es auch so für *Leucotermes* zu deuten." It seems possible, therefore, that he was mistaken regarding the position of the gonopore, relative to the position of the spermathecal furrow. A re-examination of this species would certainly be desirable.

HOLMGREN does not show any structure comparable to the interstitial fold. IMMS (1919) shows a highly developed interstitial fold in *Archotermopsis wroughtoni*. HEBERDEY (1931) felt that IMMS was mistaken regarding the presence of this structure and regarded it as a possible fixation artifact. Subsequent work by BROWMAN (1935) on *Masotermes* and *Zootermopsis*, shows the presence of a well developed interstitial fold in these two primitive genera. In both of these the interstitial fold bears sclerotized areas. BROWMAN remarks that "the interstitial fold is greatly reduced in practically all the other termites studied". AHRENS (1935, b) shows a distinct interstitial fold in *Odontotermes redemanni*. It seems probable, therefore, that IMMS' description of *Archotermopsis* is correct and this genus resembles the other primitive genera described by BROWMAN. Likewise, it is possible that HOLMGREN did not recognize the interstitial fold in *Heterotermes tenuis*, since in this species it is probably reduced and membranous.

As regards segmentation, I agree with KNOWER (1901), HEBERDEY (1931), BROWMAN (1935) and GEYER (1951), in placing the accessory gland opening on the ninth venter, the spermatheca on the eighth and the gono-

pore on the intersegmental membrane lying between the seventh and eighth. These structures, therefore, have maintained their primitive positions segmentally, although there has been a shifting anteriorly of the medial portions of the eighth and ninth venters and a shifting posteriorly of the seventh segment. HOLMGREN (1909) concludes that the spermatheca, accessory glands and the oviducts of *Heterotermes tenuis* all open through the intersegmental membrane between the seventh and eighth segments. In *Archotermopsis*, IMMS (1919) considers the intersternal fold and the floor of the inner genital chamber as the eighth segment and the entire roof of the chamber, including the apertures of the accessory gland and the spermatheca, as the ninth. These differences are more probably differences of interpretation rather than actual differences between the various genera.

The presence of a large number of ovarioles, arising along the entire length of the ovary, is in agreement with earlier observations on various Termitidae. BUGNION and POPOFF (1912) in their study of *Odontotermes* (= *Termes*) *obscuriceps*, counted 2,420 ovarioles in one ovary of a mature queen. GEYER (1951) remarks that in *Macrotermes natalensis* "the ovaries consist of a large number of ovarioles, probably several thousand in each ovary" of the young alates. The relative degree of development of the ovarioles of the young queens, as observed in *Tenuirostritermes tenuirostris* also agrees with GEYER's observations that of the large number present in *M. natalensis*, at the time of flight only the last six are well developed. In view of the large number of ovarioles which are present in these young primaries, some reconsideration must be made of the hypothesis of ovariole augmentation which has been suggested (GRASSÉ, 1949) to explain the tremendous development of certain queens and the discrepancies in the counts of the number of ovarioles in the same species as reported by different authors. In examining the young primary reproductives it is easy to misjudge the number of ovarioles, even in serial sections. In the well developed primaries on the other hand, all of the ovarioles are conspicuous and give the impression of an increased total number. BUGNION and POPOFF (1912), for example, counted the ovarioles of the mature queen by removing them one by one from the oviduct. In the serial sections of *T. tenuirostris*, on the other hand, it was necessary to use high magnification in order to distinguish the point at which each of the many immature ovarioles arose from the oviduct.

Although meiotic spindles have not been observed, all the information now at hand suggests that maturation occurs either after the deposition of the egg, or only after the oöcyte is in the final phases of development. No meiotic division figures, nor any indication of such phenomenon were found in any of the many ovarioles examined. In view of the consistent observation of mitotic figures in the germarium and various prophase stages in the initial growth region, it is difficult to feel that the process of maturation was not observed if it occurs as described by STELLA (1938). In *Kalotermes flavicollis* and *Reticulitermes lucifugus*, STELLA describes

the meiotic divisions from the more anterior oöcytes of the terminal growth region. According to her descriptions and figures, such oöcytes were still surrounded by a flattened epithelial sheath and did not contain true yolk. STELLA considered the large, central nuclei, encountered in the posterior oöcytes, as the female pronucleus. After a careful consideration of her descriptions and figures and an examination of *T. tenuirostris* and also of *Reticulitermes hesperus*, I cannot but feel that STELLA was mistaken. Certainly some confusion exists regarding her figures 3 and 4 in Plate 2,¹ which according to the legend show the first meiotic spindles of *K. flavicollis* and *R. lucifugus*, respectively. A careful comparison of these two figures shows that figure 3 is a photograph at higher magnification of a portion of the same field shown in figure 4. In the text, STELLA refers both figures to *K. flavicollis* and later refers the fourth figure to *R. lucifugus*. In my opinion, the figures show a dividing follicular epithelial cell, overlying a young primary oöcyte in the anterior portion of the terminal growth region. The large nucleus which appears in Stella's figure 4 and which she considers a pronucleus is a typical germinal vesicle of a developing oöcyte prior to yolk formation. The occurrence of a later maturation is indicated in the present observations by the persistence of a large, central germinal vesicle until long after yolk formation and by the peripheral position of an irregular nucleus in the largest yolk eggs in which a nucleus could be observed.

The structure of the testis of *Tenuirostritermes tenuirostris* resembles that of *Macrotermes* (= *Bellicositermes*) *natalensis* as described by BONNEVILLE (1936) in that the spermatid tubes are arranged in groups which empty into extensions of the vas deferens. In the case of *M. natalensis*, BONNEVILLE found that the spermatid tubes are reflexed upon themselves to form a U-shaped structure. The arch of the U is broad, and narrows towards the germarium on the one side and the basal portion on the other. The basal portions of adjacent spermatid tubes open separately into a common vas efferens. The testis is composed of a number of such clusters of spermatid tubes draining into vasa efferentia arising from the vas deferens. In *T. tenuirostris*, on the other hand, only the terminal portion of the germarium of each spermatid tube is reflexed. The basal portion of each tube is broad and the basal portions of all spermatid tubes within a testicular lobe are fused at the base. In *M. natalensis*, as in *T. tenuirostris*, there are no accessory structures associated with the male reproductive system. The sperm are apparently stored in simple enlargements of the basal portions of the vasa deferentia.

GEYER (1951) describes the male reproductive system of *Macrotermes natalensis*. According to present synonymies (A. E. EMERSON, personal correspondence), *Bellicositermes natalensis* is a synonym of *Macrotermes natalensis*. That is, the species studied by BONNEVILLE (1936) is synonymous with that later considered by GEYER. The descriptions of the male reproductive systems, however, are extremely dissimilar. GEYER does not describe the form of the individual spermatid tubes. He states that

the testes are "irregular structures, hollow in the centre. The testicular tubules open into these cavities and the vasa deferentia also originate from the posterior third of the testes." As regards the basal portions of the vasa deferentia, GEYER describes basal, anteriorly directed pouches arising from the vasa deferentia. He considers these pouches to be "simple saccular mesadenia" which have "attained the secondary function of vesiculae seminales since the primary vesiculae seminales are absent". These pouches were also present in *M. swartzii* as well as in the more primitive *Neotermes zuluensis* and *Kalotermes durbanensis*. GEYER does not make any direct comparisons between his observations and those of BONNEVILLE although he mentions the latter work. It is not possible, on the basis of the information now available, to resolve the differences in the descriptions by these two authors for what is reported to be the same species.

In the case of those reproductives of the Termitidae which have been described, there are a larger number of generative elements in the testis and the ovary than are encountered in those species described from the more primitive families. In the latter, the ovarioles do not usually exceed 50 in each ovary and there are usually only six to ten spermatid tubes in each testis. In the Termitidae, at least 400-500 ovarioles are present and there may be as many as several thousand in each ovary in some species. Likewise, the number of testicular elements has increased to 40 or more spermatid tubes.

Summary.

The reproductive system of *Tenuirostritermes tenuirostris* shows many of the features that have been attributed to other species of the Termitidae. In the female, the eighth and ninth sternite are reduced to lateral plates, connected by a chitinous membrane. The genital chamber is divided into two regions, a broad outer chamber posteriorly, and an inner, narrower chamber anteriorly. The accessory gland opens into the outer genital chamber via an unsclerotized orifice at the medial, anterior portion of the ninth sternite. Beneath and lateral to this aperture lie two unsclerotized projections from the eighth sternite, the ventral valves. At the base of the ventral valves lies the opening of a heavily chitinized groove, the spermathecal furrow. At this point the genital chamber is compressed laterally to form the inner genital chamber. The spermathecal furrow extends anteriorly for 120 to 140 microns to the mid-point of the roof of the inner genital chamber. It is continuous anteriorly with a closed duct which runs medially along the inner, dorsal wall of the inner genital chamber and joins the spermatheca. The spermatheca arises at right angles to the duct and runs dorsally. The inner wall of the spermatheca is perforated by numerous, minute, intracellular canals which extend into the secretory columnar epithelium. The spermathecal furrow, duct and the spermatheca all lie within the eighth segment. Dorsolaterally,

in the wall of the inner genital chamber, lie two narrow, sclerotized bars, the basivalvulae. The floor of the inner genital chamber is composed of the intersegmental membrane between the seventh and eighth segments. This membrane is perforated by the gonopore, the posterior margin of which lies opposite the aperture of the spermathecal duct. The posterior ventral margin of the inner genital chamber is marked by an intersternal fold which is unsclerotized. The seventh sternum forms the sub-genital plate. Each ovary includes 400-450 ovarioles, arising from all sides and along the entire length of the oviduct which extends anteriorly into the first or second abdominal segment. In the male, the eighth and ninth sternites are reduced but entire. There are no styli on the ninth sternum. No accessory structures are associated with the ejaculatory bulb or with the vasa deferentia. Each testicular lobe is a compound structure, including a number of spermatic tubes which are fused at the base but terminate individually in a recurved germarium.

Zusammenfassung.

Das Genitalsystem von *Tenuirostritermes tenuirostris* hat manche Eigenschaften, welche andern Termitiden-Arten zugeschrieben worden sind. Im Weibchen sind die achte und neunte Sterna zu Seitenplatten reduziert und mit einer chitinösen Membran verbunden. Der Genitalraum ist in zwei Bezirke abgeteilt; davon ist der hintere Bezirk ein breiter, äußerer Raum, während der vordere Bezirk ein innerer, schmaler Raum ist. Die akzessorische Drüse öffnet sich in den äußeren Genitalbezirk durch eine unsklerotisierte Öffnung am medialen vorderen Teil des neunten Sternits. Ventral und zugleich seitlich von dieser Öffnung liegen zwei unsklerotisierte Fortsätze vom achten Sternit, die Ventralklappen. An der Basis der Ventralklappen befindet sich die Öffnung einer stark chitinösen Rinne, die Samenrinne. An diesem Punkt ist der Genitalraum seitlich zusammengedrückt und bildet den inneren Genitalraum. Die Samenrinne setzt sich um 0,120 mm bis 0,140 mm vorwärts bis zum Mittelpunkt des inneren Genitalraumes fort. Diese Rinne setzt sich vorwärts in einen geschlossenen Kanal fort, welcher median an der inneren dorsalen Wand des inneren Genitalraumes verläuft und sich an die Samenkapsel anschließt. Die Samenkapsel entspringt rechtwinklig zum Kanal und setzt sich dorsalwärts fort. Die innere Wand der Samenkapsel ist von zahlreichen kleinen intrazellulären Kanälchen durchbohrt, welche sich in das hohe Säulenepithel fortsetzen. Dorsolateral in der inneren Wand des inneren Genitalraumes liegen zwei schlanke sklerotisierte Bänder, die *Basivalvulae*. Der Boden des inneren Genitalraumes besteht aus der intersegmentalen Membran zwischen dem siebten und achten Segment. Diese Membran ist von der Geschlechtsöffnung, deren hinterer Rand der Öffnung des Samenkanals gegenüber liegt, durchbohrt. Der hintere ventrale Rand des inneren Genitalraumes ist von einer unsklerotisierten Intersegmentalfalte begrenzt. Das siebte Sternit bildet die Subgenitalplatte. Jedes Ovar umfaßt 400—

450 Ovariolen, welche von allen Seiten und der ganzen Länge des Eileiters entlang entspringen. Der Eileiter setzt sich vorwärts bis in das erste oder zweite Abdominalsegment fort. Im Männchen sind das achte und neunte Sternit kleiner und ungeteilt. Am neunten Sternit befinden sich keine Styli. An den *Vasa deferentia* oder an der Ejakulationsblase finden sich keine akzessorischen Strukturen vor. Jeder Hodenlappen ist eine zusammengesetzte Struktur, welche eine Anzahl Samenröhrchen, welche an der Basis zusammen gewachsen sind aber individuell in einem gebogenen Germarium endigen, umfassen.

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THE PRODUCTION AND REPLACEMENT OF SOLDIERS IN INCIPIENT COLONIES OF *RETICULITERMES* *HESPERUS* BANKS

by

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Most of the studies of caste determination in the Isoptera have been concerned with the production of replacement reproductives. Little information has been obtained regarding the production of individuals of the soldier caste. CASTLE (1934) found that in 45 incipient colonies of *Zootermopsis angusticollis* (Hagen), each produced a soldier within 75 days after the hatching of the first egg and no further soldiers appeared in these colonies during the first year. CASTLE devised an experiment to test: *a.* the ability of the young colony to produce a second soldier if the first one was removed, and *b.* the suppression of soldier production if a soldier-nymph was introduced before the young colony had produced its own soldier.

These experiments demonstrated that more than one of the individuals produced during the first year are capable of becoming soldiers. In 6 of 12 colonies from which the initial soldier was removed, a second soldier was produced. Upon the removal of this second soldier, 4 of 6 colonies produced a third soldier. Two of these 4 colonies produced a fourth soldier upon the removal of the third and 1 of these 2 colonies produced a fifth soldier upon the removal of the fourth. The reciprocal groups, which had received a soldier-nymph, showed a definite suppression of soldier production.

LIGHT (1942-1943) encountered a high initial soldier production in young colonies of *Zootermopsis nevadensis* (Hagen). At that time LIGHT made the generalization that "at least one soldier is present in the first broods of all termites, the development of whose incipient colonies is known". It is now evident that this was an over generalization which cannot be applied to *Reticulitermes*. PICKENS (1932 *a*) does not state the actual number of his colonies of *R. hesperus* Banks which produced a soldier. He does remark that "small colonies, all hatched from one mother, may not produce a soldier for as much as two years." BUCHLI (1950), in his study of *R. lucifugus* (Rossi), obtained an incipient soldier in 20 % of his laboratory colonies.

The present paper is concerned with groups of *R. hesperus* which were

maintained by the late Professor S. F. LIGHT. No attempt was made to follow the exact development of these colonies which were utilized for testing culture methods and were employed as source colonies for later experimental groups. The colonies were examined at various intervals and a general picture of their initial development is available. Of particular interest and significance is the incidence of soldiers in these colonies and a repetition of a portion of CASTLE's experiment for soldier replacement.

DEVELOPMENT OF THE COLONIES

All of the primaries utilized for the culture groups were obtained after normal emergence following the early autumn rains. The alates for series RHI were obtained from Rest Haven, Mendicino County, California. All other alates were obtained from various flights in Berkeley, Alameda County, California. Tandem "pairs" were utilized for setting the groups and many of these were later found to be couples of males or couples of females. The colonies were maintained in various modifications of the "standard" Monterey pine and agar-agar culture method (LIGHT and WEESNER, 1947), utilizing 1 dram, screw-capped vials as containers.

Table 1 presents a summary of the groups to be considered. Of the seven series of cultures, IMV and IN are so small that they will not be discussed in any detail. It should be noted that the period from the appearance of the first egg to the appearance of the first young does not necessarily indicate the time required for egg development, since the records are not continuous enough to permit such a conclusion. In the following accounts of colony development, the days indicated refer to the number of days which have elapsed since the pairs were set in culture. Only the data for initial development are included, except to indicate the later production of soldiers.

Series BRI (64 colonies). No eggs were present at the first observation on the sixth day. At the second observation, 29 days after pairing, 4 colonies each had 1 egg and 1 colony had 2 eggs. At the third observation, 34 days after pairing, a total of 12 eggs was observed in 8 colonies with a maximum of 4 in 1 colony. At 47 days a total of 35 eggs was present in 16 colonies with a maximum of 5 eggs in 1 colony. At 68 days there were 43 eggs in 10 colonies (maximum of 7 eggs) and, in addition, 11 colonies had a combined total of 17 young with a maximum of 4 in 1 colony. At 78 days, 138 eggs were counted in 24 colonies (maximum 11) and a total of 41 young was present in 21 colonies (maximum 5). The maximum combined population, eggs and young, at 78 days was 13. At 116 days no count was made of the young but an increased number of first-instar individuals was noted. At 123 days the colonies were transferred to fresh media. At this time there was a total of 177 young in 28 colonies (maximum 13) and 105 eggs in 25 colonies with a maximum of 11 eggs in 1. The maximum combined population (eggs and young)

TABLE 1.

Summary of the Data for the Incipient Colonies.

CULTURE series.	NUMBER set.	NUMBER considered (1).	NUMBER producing a Soldier.	DAYS AFTER PAIRING TO.		
				First observed egg.	First observed young.	First observed Soldier-Nymph.
BRI	84	64	3	29	68	174
IMM	37	28	12	26	58	113
IM	57	43	4	16	60	115
RHI	29	26	8	48	74	202
BMI	49	31	6	27	69	123
IMV	8	7	1	15	58	126
IN	6	5	0	?	77	—
Total		204	34			
(1) Number set minus initial deaths and couples of males or couples of females.						

at 123 days was 17. Three groups from this series subsequently produced a soldier-nymph between 174 and 196 days after pairing.

Series IMM (28 colonies). No eggs were present at the first observation, 15 days after pairing. At 26 days a total of 30 eggs was present in 14 colonies, with a maximum of 3 in 1 colony. At 40 days a total of 61 eggs was present in 21 colonies (maximum 5). At 58 days a total of 73 eggs was present in 21 colonies (maximum 7) and, in addition, a total of 48 young was present in 20 colonies (maximum 5). At 72 days, 84 eggs were counted in 21 colonies (maximum 7). At 89 days, 88 eggs were present in 22 colonies (maximum 8) and 142 young in 25 colonies (maximum 10). At 113 days, a soldier-nymph appeared in each of 7 colonies and 2 more appeared in additional groups at 116 days. Three more soldiers were produced by this series of colonies, 1 at 125 days, 1 at 134 days and the last at 146 days after pairing.

Series IM (43 colonies). One egg was present in a single colony at the first observation, 16 days after pairing. At 27 days a total of 24 eggs was present in 14 colonies (maximum 4). At 39 days a total of 56 eggs was present in 22 colonies (maximum 5). At 60 days, 86 eggs were present in 25 colonies (maximum 6) and, in addition, there was a total of 35 young in 22 colonies (maximum 4). At 74 days, 120 eggs were present in 27 colonies (maximum 8) and 59 young in 27 colonies (maximum 6). At 93 days, a total of 208 eggs was present in 31 colonies (maximum 11)

and 119 young in 29 colonies (maximum 10). The maximum combined population at 93 days, that is, eggs and young, was 18. Two soldier-nymphs appeared at 115 days and 2 additional soldiers at 178 days.

Series RHI (26 colonies). No eggs were observed at the first observation, 28 days after pairing. At 48 days, 4 colonies each had a single egg. At 60 days a total of 10 eggs was present in 6 colonies (maximum 2). At 74 days a total of 7 eggs was present in 6 colonies and, in addition, 9 young were present in 8 colonies. At 94 days, 70 eggs were present in 11 colonies (maximum 8) and a total of 10 young in 9 colonies. At 105 days, 93 eggs were present among 11 colonies (maximum 10) and a total of 12 young in 11 colonies. The maximum combined population of eggs and young in a single colony at 123 days was 15. When the colonies were transferred to fresh culture media at 151 days there were 107 young present in 12 colonies (maximum 8) and 45 eggs in 8 colonies (maximum 8). Eight of the colonies of the RHI series subsequently produced a soldier. Two colonies had soldier-nymphs at 202 days, three more appeared at 215 days, another at 223 days, one at 245 days and the last at 258 days.

Series BMI (31 colonies). One egg appeared in a single colony 27 days after pairing and another in a second colony at 30 days. At 41 days a total of 20 eggs was observed in 7 colonies (maximum 4). At 69 days, 51 eggs were present among 18 colonies (maximum 8) and, in addition, 26 young were present in a total of 13 colonies (maximum 3). At 86 days a total of 97 eggs was present in 21 colonies (maximum 10) and a total of 74 young in 24 colonies (maximum 6). At 100 days a total of 109 eggs was present in 18 colonies (maximum 12) and 106 young in 23 colonies (maximum 8). Soldier-nymphs appeared in each of 3 colonies at 123 days and in 3 additional colonies at 125 days.

SOLDIER REPLACEMENT

Despite the relatively low incident of soldiers in these colonies, as compared with CASTLE's (1934) observations for *Zootermopsis angusticollis*, it seemed desirable to test the ability of the incipient colony of *R. hesperus* to replace the loss of the initial soldier. The soldier-nymph which was produced in each of 13 colonies was removed from its colony of origin and introduced into a similar colony which had not yet produced a soldier. These colonies were selected from among culture series IMM and BMI, where the initial soldier-nymphs appeared 116 to 123 days after pairing. The transfer of soldier-nymphs was made at 121 days after pairing for cultures from the IMM series and at 125 days for cultures from the BMI series. The two groups of colonies, one from which the soldier-nymphs had been removed and the second into which the soldier-nymphs had been introduced, were maintained for one year after the initiation of the experiment. At the time of the transfer each of the colonies contained a

few eggs, a number of first- and second-instar young, from 1 to 6 third-instar young and a pair of primary reproductives.

One of the soldier-nymphs which had been introduced into a new colony did not survive the transfer. The other 12 were apparently accepted by the recipient colonies although some of them were lost between 3 and 12 months after the transfer. No new soldiers appeared in any of the 13 colonies. At the end of one year, there were 11 surviving colonies, 9 of which contained a single soldier and 2 of which lacked a soldier.

Of the 13 colonies from which the soldier-nymph had been removed, one died immediately after resetting. Of the 12 which survived, 6 produced a replacement soldier (table 2). The first replacement soldier-nymph appeared 44 days after the removal of the initial soldier-nymph. Soldier-nymphs were subsequently observed in 2 additional colonies, 1 at 56 days and 1 at 69 days. Seventy three days after the initiation of the experiment, a callow soldier was observed in a fourth colony. At 83 days, two additional colonies contained a replacement soldier. It should be noted that the replacement soldiers all appeared between 160 and 208 days after the pairing of the reproductives, or at the time when some of the colonies (table 1) were producing their first soldier. The 6 colonies which did not produce a replacement soldier survived for the full year of the experiment.

TABLE 2.

Data for Six Colonies Producing a Replacement Soldier.

CULTURE number.	DAYS from Removal of Soldier-Nymph to observation of replacement individual.	TYPES of individuals observed.	DAYS AFTER PAIRING TO.	
			Initial Soldier-Nymph.	Replacement individual.
BMI-48	44	Soldier-Nymph.	123	169
BMI-1	56	Soldier-Nymph.	123	181
IMM-34	69	Soldier-Nymph.	116	190
IMM-4	73	Callow Soldier.	123	194
IMM-28	83	Soldier.	116	204
BMI-43	83	Soldier.	123	208

It is possible that had the experimental groups retained the initial soldier, produced from the first group of young, they might also have produced a second soldier from among the second group of young. If we eliminate those colonies where the initial soldier was derived from the second group of young, as well as those from which the soldier was removed, we have a second control series which produced a soldier at the same time as the initial soldier in the experimental series. Four of the colonies in series IM, 6 in series IMM and 1 in series IMV, or a total of 11 colonies,

produced and retained an initial soldier from the first group of young. None of these produced a second soldier from the subsequent group of young. It seems reasonable, therefore, to conclude that the production of a second soldier in 50 % of the experimental colonies was a direct effect of removing the initial soldier.

DISCUSSION

Although the data available for the initial development of the colonies are general in nature they do exhibit several consistent features: 1. There is a small initial deposition of eggs between 15 and 60 days after pairing which is followed by a secondary flare of egg deposition, usually between 70 and 100 days after pairing. 2. Some colonies produced a soldier very early in colony development and these must be derived from the initial groups of eggs and young. 3. In other colonies a soldier appears much later and is apparently derived from the second group of eggs deposited between 70 and 100 days after pairing. 4. The production of soldiers during the first year varies from one group of colonies to another. 5. The incidence of a soldier among all of the colonies during the first year is relatively low, the average production in 204 colonies being 16 % with a maximum of 42 % in culture series IMM.

The erratic production of soldiers in these colonies suggests that either abnormalities were occurring under the existing laboratory conditions or that the conditions which are prerequisite for soldier production do not occur in all young colonies. A careful consideration of the data available for these groups failed to suggest any consistent variation such as size, rate of development, etc., between colonies which were soldierless as compared with those which did produce a soldier. Certainly the data did not suggest that some were "normal" and others "abnormal" unless the soldier itself is to be taken as an indication of normality. This latter assumption does not seem a safe one without supporting data. Furthermore, a consideration of PICKENS' data (1932 *a*) for the same species, reveals that the soldiers which he obtained appeared much later than did most of those in the present colonies. Indeed, PICKENS concluded that the soldiers produced by his colonies must have been derived from the last eggs which were deposited by the young pair. PICKENS (1932 *a*, 1932 *b*) states that these eggs were laid somewhat after most of the eggs had been deposited, and required a longer period to develop than did the earlier eggs.

In view of the low initial incidence of soldiers, the data obtained on soldier replacement are extremely interesting. Whereas the average production of soldiers in the present cultures was 16 % and the highest initial soldier production was 42 % in any series of cultures, 6 of the experimental group of 12 colonies produced a second soldier when the first one was removed. This incidence of soldier replacement is comparable to that obtained by CASTLE (1934) with the same number of colonies of *Zooter-*

mopsis angusticollis, even though in this species there was a 100 % initial soldier production in the undisturbed colonies. The failure of the groups to produce a soldier when a foreign soldier was introduced is of much less significance here than in Castle's groups, since, again, the initial spontaneous soldier production in *R. hesperus* was much lower than in *Z. angusticollis*. In any case, no second soldier did appear in groups which already possessed a soldier, either normally or by introduction.

The data now at hand indicate that in laboratory colonies of *R. hesperus*, initiated by a pair of primary reproductives and maintained at the same time and under the same conditions, some have a greater tendency to produce soldiers than do others. Furthermore, it is evident, that not all colonies produce a soldier during the first year.

It should be noted that the pattern of egg deposition in the present series of colonies does not agree with that described by PICKENS for the same species. PICKENS (1934) states that "an average of less than ten are produced in the first clutch. The number may be as low as four or six, or as high as fifteen, or in rare cases twenty. The eggs are laid at fairly regular intervals. A period of from one to three days elapses between the deposition of two successive eggs, except for the last two or three, which are laid at increasingly long intervals, of as much as a week or tens days".

The pattern of egg deposition for *R. hesperus* differs strikingly from that which BUCHLI (1950) found in *R. lucifugus*. In the latter species, 10 to 20 eggs are deposited within a month and egg deposition terminates when the first young appears, about 28 days after the deposition of the first egg. In *R. hesperus*, on the other hand, the secondary flare of egg production usually coincides with the hatching of the first eggs.

Summary.

1. Only a small percentage of incipient colonies of *Reticulitermes hesperus* produce a soldier during the first year.
2. In some colonies the soldier is derived from the first eggs and in other colonies the soldier develops from later eggs.
3. Not more than one soldier was present in any one colony during the first year.
4. If the initial soldier, produced from the first group of young was removed, a second or replacement soldier was produced from the second group of young in 50 % of an experimental series of 12 colonies.

Zusammenfassung.

1. Nur in wenigen der jungen Kolonien von *Reticulitermes hesperus* erscheint ein Soldat während des ersten Jahres.

2. In manchen Kolonien entwickeln sich die Soldaten aus den ersten Eiern, während sie sich in anderen Kolonien aus späteren Eiern entwickeln.

3. In jeder Kolonie wurde im Lauf des ersten Jahres nur ein einziger Soldat gefunden.

4. Wenn der aus der ersten Gruppe von Jungen stammende Soldat zerstört wurde, so entwickelte sich aus der zweiten Gruppe von Jungen in 50 % einer Gruppe von 12 Experimentalkolonien, ein zweiter Soldat.

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II

NOUVELLES DE L'UNION

COMPTE RENDU DU CONGRÈS DE WURZBURG

Du 3 au 6 avril 1955, 219 congressistes ont été les hôtes de Würzburg sur invitation de la section allemande. Le Congrès s'est déroulé dans une atmosphère extrêmement sympathique, et les échanges intellectuels y ont été fructueux.

Aux nombreuses séances scientifiques se sont ajoutées de magnifiques réceptions, et c'est avec regret que les congressistes se sont séparés après l'excursion sur la « Romantische Strasse ».

Tous les congressistes ont demandé que l'ensemble des communications lues au cours du Congrès soit publié dans le cadre de la revue *Insectes Sociaux*. Dès leur retour en France, M. le professeur Grassé et le secrétaire ont soumis la question aux éditeurs de la revue. Mais la subvention de 1 000 Deutschmarks transmise par la section allemande était loin de couvrir les frais d'édition d'un volume de plus de 200 pages. Le Comité d'édition a alors décidé de publier les comptes rendus dans les nos 1 et 2 du tome III d'*Insectes Sociaux* qui doit paraître au début de l'année 1956. *Ce volume sera servi sans majoration de prix à tous les abonnés ; il pourra être obtenu séparément dans les limites du stock disponible par tous ceux qui en feront la demande à la Librairie Masson.*

Pendant le Congrès s'est tenue une réunion d'administration de l'U. I. E. I. S. dont on trouvera le compte rendu ci-dessous.

Il faut à nouveau exprimer à la section allemande, à son président M. le professeur K. Gösswald et à son secrétaire le Dr W. Kloft, toute la gratitude des congressistes et les assurer que Würzburg restera une étape importante dans le développement de l'Union.

RÉUNION ADMINISTRATIVE DE L'U. I. E. I. S. WÜRZBURG, 6 AVRIL 1955

Présents :

Membres du Comité directeur :

MM. BRIAN (Grande-Bretagne), CHRISTENSEN (Scandinavie), GÖSSWALD (Allemagne), GRASSÉ (France), JUCCI (Italie), SCHNEIRLA (U. S. A.).

MM. RAIGNIER (Bénélux) et UCHIDA (Japon), empêchés de venir au Congrès, avaient fait parvenir leurs excuses au Secrétariat.

Membres de l'Union :

MM. Carthy (Grande-Bretagne), Harris (Grande-Bretagne), Kloft (Allemagne), Kutter (Suisse), Lüscher (Suisse), O'Rourke (Irlande), Stumper (Luxembourg), Richard, secrétaire (France).

I. — Vie de l'Union.

L'Union se développe constamment. Après la création d'une active section japonaise (voir *Insectes Sociaux* n° 3, tome II), une section brésilienne a vu le jour sous la présidence du Dr J. S. Moure. M. Christensen a pu étendre la section danoise qu'il a transformée en section scandinave. M. Carthy s'occupe activement de la création d'une section britannique ; celle-ci doit être constituée prochainement.

Nous avons dépassé le nombre de 300 membres, mais il est nécessaire d'étendre toujours davantage le rayonnement de l'Union.

Les cotisations des membres sont payées assez régulièrement par la plupart des grosses sections, mais certaines sont encore en retard ; par contre, les frais de correspondance grèvent lourdement le budget de l'Union.

Une nouvelle série de timbres pour les cartes de membre sera imprimée pour 1956, avec le même système de distribution par les secrétaires de sections.

II. — Prochain Congrès.

Le Congrès d'Entomologie étant fixé au mois d'août 1956 à Montréal, les présents décident de réunir le prochain Congrès de l'U. I. E. I. S. en 1957.

Une réunion administrative de l'U. I. E. I. S. se tiendra au cours du Congrès de Montréal, et le Secrétaire est chargé de se mettre en rapport avec le Secrétariat du Congrès d'entomologie pour demander la création d'une section d'*Insectes Sociaux* dans le cadre du Congrès.

Diverses propositions sont faites pour le Congrès de 1957. Les présents demandent unanimement qu'il se tienne à Paris. La réunion de prochains Congrès à New-York et à Londres est envisagée. De toute façon, les présidents de sections doivent faire connaître au plus tôt au Secrétariat général l'avis et les suggestions de leur section sur le lieu et le déroulement du Congrès.

Dès maintenant, M. Grassé avertit ses collègues que les pouvoirs du bureau élu en 1952 se terminent au Congrès de 1957 et qu'il faudra alors procéder à de nouvelles élections.

M. O'Rourke et divers autres membres de l'Union demandent qu'on perçoive une cotisation pour le prochain Congrès. Cette cotisation devra assurer le service gratuit du volume des communications.

III. — Bulletin.

Après un an d'exercice, la Librairie Masson a communiqué le bilan de gestion du Bulletin. Ce bilan fait apparaître un déficit d'une centaine de mille francs. En ce qui concerne les prévisions pour l'année 1955, si la Librairie Masson continue à bénéficier de subventions comme par le passé, la revue doit approcher de son équilibre financier. Mais il faut remarquer que les membres de l'Union s'abonnent très peu au Bulletin : actuellement, un membre sur trois seulement est abonné.

Le seul moyen d'équilibrer le budget du Bulletin et d'augmenter son volume et son rayonnement est de faire toujours de nouveaux abonnés.

INFORMATIONS

British Section.

A meeting was held at Queen Mary College, London, on June 20th. 1955, at which a British Section of the International Union was inaugurated. The constitution of the Section was drawn up and accepted at another meeting at Imperial College, London, on November 2nd. 1955. Dr J. D. CARTHAY was elected President and Dr C. G. BUTLER Secretary of the Section.

TRAVAUX PUBLIÉS PAR DES MEMBRES DE L'UNION

LÖKEN (Astrid). — Bumble Bees in Relation to *Aconitum septentrionale* in Central Norway (Oyer) (**Nytt Magasin for Naturvidenskapene**, **87**, Oslo, 1949). — Bumble Bees in Relation to *Aconitum septentrionale* in Western Norway (Eidfjord) (**Norsk Entomologisk Tidsskrift**, **8**, 1950). — Insects valuable for pollination in orchards (in Norwegian) [**Frukt og Bær**, 1949, Oslo]. — Pollinating insects and the climatical influence on their fieldwork (in Norwegian) [**Frukt og Bær**, 1951, Oslo]. — Observations of Bumble Bee Activity during the Solar Eclipse June 30, 1954 (**Universitetet i Bergen Arbok 1954, Naturvitenskapelig rekke nr. 13**, Bergen, 1954).

The weather conditions with nearly constant temperature and humidity at the same time as it remained overcast all the day and with the light intensity as the only variable factor of importance, constituted a favourable situation from an ecologist's point of view. A diagram reveals that the *Bombus* activity declined gradually and all individuals, apart from a single specimen, had disappeared when the total eclipse occurred. The specimen, left, was heard for another minute. 9-10 minutes went by before they returned to the field after the total eclipse. The fact that also normally the bumble bees need a higher light intensity for starting their field work in the morning than to fulfil similar duties at night and other factors influencing this activity are stressed.

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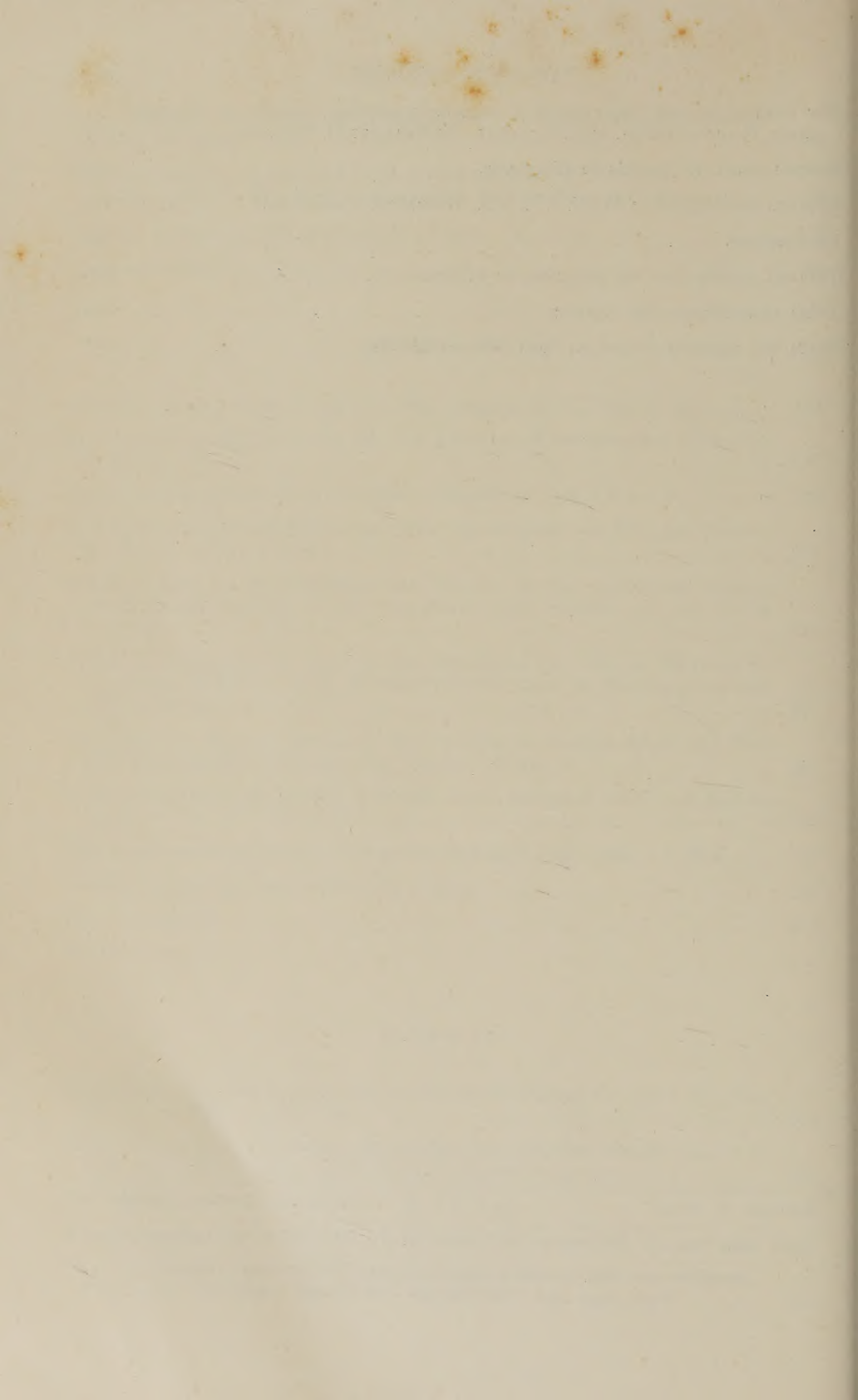
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